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A GENETIC STUDY OF WHEAT×RYE HYBRIDS AND BACK CROSSES[1]

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INTRODUCTION

A number of present-day wheat breeders are back crossing wheat ×rye hybrids as a possible means of improving winter wheat. Although bread wheats are superior in quality to rye, some rye varieties possess certain characters, such as winter hardiness, which would be very valuable if they could be transferred to wheat. A limited degree of success in transferring rye characters to wheat has been achieved, but the manner of transmission is not definitely known. The high degree of sterility characteristic of wide crosses such as that between wheat and rye has not been overcome completely in the new strains possessing rye characters. The main objects of the experiments here reported were to obtain further information on the manner in which rye characters may be transferred to wheat and to study the degree and causes of sterility and the relationship of characters in successive generations of hybrids.

REVIEW OF LITERATURE

There is a considerable body of literature on experiments with wheat×rye hybrids. A fairly complete review of such experiments has been made by Bleier (*2*)[3] and others. Only those references which have a bearing on the present paper will be cited here.

The wheat×rye cross[4] usually is not difficult to accomplish, but until recently the reciprocal cross has been considered impossible. Many workers report only a low percentage of kernels from wheat ×rye crosses, while others report a high percentage. Backhouse (*1*), using a Chinese wheat supplied by Biffen, reported percentages up to 80. Thompson (*16*), utilizing the same wheat, stated that it was not difficult to get 90 per cent of crossed kernels in P_1. Nina Meister and Tjumjakoff (*13*) reported up to 60 per cent. Leighty and Sando (*10*), also crossing a Chinese variety with rye, obtained a 90.5 per cent set of seed. The variety of Chinese wheat used by Leighty and Sando has a clavate spike and is red kerneled, while the one used by

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[3] Reference is made by number (italic) to Literature Cited, p. 338.

[4] In the designation of a cross the female parent will appear first throughout this paper.

Backhouse and Thompson has a fusiform spike with white kernels. Poor results from crossing no doubt may be due in part to variation in compatibility to rye in different varieties of wheat. Firbas (*4*) crossed a number of varieties of wheat with several varieties of rye and found distinct differences among the wheats.

In 1922 Gaines and Stevenson (*6*) reported maternal inheritance in a rye×wheat cross. The plants were ryelike and had only a moderately high degree of sterility. The chief criterion of hybridity employed by these investigators was susceptibility to disease, which was not observed in the rye parent.

Nina Meister and Tjumjakoff (*13*), in 1927, succeeded in making rye×wheat crosses. From 3,894 crossed rye florets, 96 kernels, or 2.5 per cent of the total number, were obtained. The hybrids were identical with the usual F_1 wheat-rye crosses. The authors attributed their success to the use of a specially constructed greenhouse where the plants were grown. Maintenance of proper humidity for the germinating wheat pollen was considered an important factor.

Wheat normally is self-fertilized and rye cross-fertilized. The earlier breeders usually obtained some fertility in F_1 crosses. Jesenko (*7*) appears to have been the first to make a definite contribution to the knowledge of sterility relationships in the hybrids. The F_1 hybrids do not dehisce and shed their pollen, as both wheat and rye normally do. Jesenko opened the anthers artificially and applied the pollen to the florets of the hybrid. One kernel was obtained, which he later concluded must have resulted from chance pollination by wheat. The following year about 3,000 florets of the F_1 were again selfed. Not a single kernel was obtained. Since the pollen of wheat as well as of rye may be carried about by winds at blossoming time, he concluded that the progeny reported by other workers must have been due to chance fertilization by such pollen.

Meister (*12*) isolated 220 heads of natural wheat×rye hybrids at blossoming time. All were entirely sterile.

Leighty and Taylor (*11*) bagged 176 individual heads and compared their fertility with that of 309 unbagged heads. The former were completely sterile, while in the latter a fertility of 0.66 per cent was observed.

Since F_1 hybrids were thus definitely proved to be sterile, the chance pollinations found largely determined the direction of further investigation of wheat×rye hybrids. Jesenko (*8*) compared both the wheat and the rye parent in back crossing on the hybrid. With the wheat back crosses he obtained from three to six kernels per 1,000 florets pollinated. In 1912 one kernel was obtained from 4,800 F_1 flowers back crossed with rye, the plant produced being ryelike.

The main effort of plant breeders working with hybrids of wheat and rye has been directed to the improvement of wheat. For this purpose hybrids from chance pollinations and from artificial back crosses with wheat have been used. Efforts are being made to fix desirable rye characters in true-breeding back-crossed strains. Meister (*12*), in 1921, reported segregation for frost resistance in winter wheat×winter rye crosses, and in a verbal statement in 1927 he reported true-breeding strains of winter wheats of increased hardiness. Leighty and Taylor (*11*) reported the occurrence of three apparently true-breeding "hairy-neck" strains in the F_6 progeny of an F_5 wheat×rye hybrid.

PARENT VARIETIES

The original crosses used in these experiments were made between seven varieties of wheat and two of rye. Experimental data collected in the later generations were confined to three crosses involving Rosen and Dakold ryes and Kanred and Hybrid 128 wheats. The rye varieties were obtained from the Dickinson substation, Dickinson, N. Dak. The wheats were pure lines obtained from varieties previously grown by the writer in experiments at University Farm, Davis, Calif.

ROSEN RYE

Rosen rye (*Secale cereale* L.), C. I.[5] 195, was obtained originally from Russia in 1908 by the Michigan Agricultural Experiment Station as an unnamed variety (*14*). It is a slightly hardy winter variety with comparatively short, faintly purple to purple, stiff straw, broad leaves, and broad, flat, dense heads. The peduncle immediately below the head usually has a dense coat of hair or pubescense for a distance of about 2 inches. The term "hairy neck," first applied to this character by Leighty and Taylor (*11*), will be used in the present paper. The kernels are normally 7.5 mm. long but vary in different seasons. In the experiments here reported, the kernel color usually was pale red or yellowish; but gray and green kernels nearly always were present. Rosen rye is slightly more winter hardy than Kanred wheat.

DAKOLD RYE

Dakold rye (*Secale cereale* L.), N. Dak. No. 959, is an early-maturing winter variety developed at the North Dakota Agricultural Experiment Station (*15*). In early growth it is more prostrate than Rosen and has narrower leaves. The stems are slender, medium tall, and light purple to purple in color, with strong hairy necks. The spikes are slender, and the kernels are dark reddish yellow or greenish, and small, averaging about 7 mm. in length. Dakold is known particularly for its winter hardiness.

KANRED WHEAT

Kanred wheat (*Triticum vulgare* Vill.), C. I. 5146, has a distinctly prostrate winter habit with fine dark-green leaves, is midseason in maturity, and has white, weak, mid-tall stems with glabrous peduncles. The spikes are awned, fusiform, mid dense; the glumes glabrous, white; and the beaks from 3 to 25 mm. long. The kernels are red and vary from 6.5 to 6.9 mm. in length. Kanred is moderately winter hardy.

HYBRID 128 WHEAT

Hydrid 128 wheat (*Triticum compactum* Host.) was originated at the Washington Agricultural Experiment Station from a cross between Jones Winter Fife (*T. vulgare* Vill.) and Little Club (*T. compactum* Host.) (*3*). It is a uniform, constant, true-breeding, winter-habit, mid-season variety with white, stiff, strong, mid-tall stems and glabrous peduncles. The spikes are dense, erect, with short-tip awns, and the glumes are glabrous, white, with beaks 0.5 mm. long. The kernels are white and vary from 5.6 to 5.8 mm. in length. Hybrid 128 is a tender winter wheat.

[5] C. I. denotes accession number of Office of Cereal Crops and Diseases, formerly Office of Cereal Investigations.

OTHER VARIETIES

A number of other wheats and wheat allies were crossed with rye in the initial stages of the experiment. No description of these will be given. They included Red Winter spelt (*Triticum spelta* L.), C. I. 1772; Peliss (*T. durum* Desf.), C. I. 1584; Clackamas (*T. durum* Desf.), C. I. 6241; Black Winter emmer (*T. dicoccum* Schrk.), C. I. 2337; and Polish wheat (*T. polonicum* L.), C. I. 3001.

EXPERIMENTAL METHODS AND DATA

All the hybrid and parental material, except a limited number of plants grown at Berkeley for cytologic study in 1929, was grown in the cereal nursery at University Farm, Davis, Calif. As the parental varieties were of winter habit, only one generation was grown each year. All sowings were made in the fall, mostly in November. Seed from the F_1 and the P_1 back-crossed generations was spaced 4 to

FIGURE 1.—Bagged second back-cross second-generation plants of Hybrid 128 wheat × Rosen rye, Davis, Calif., 1928

6 inches apart in rows 1 foot apart, and the segregating generations (1928–29) 2 inches apart in the rows.

In making crosses and back crosses common white paper or glassine bags were used to protect emasculated and pollinated heads from chance pollination. All plants from back-crossed kernels and two selfed generations (in the period from 1925–1928) were covered with 30-pound manila paper bags to prevent chance pollination. (Fig. 1.) Each plant was tied to a stake. Development appeared to proceed in a fairly normal manner in covered plants, although there was some reduction in vigor and fertility.

At harvest the plants were pulled and taken to the laboratory for description and study. The characters studied in most of these plants include color of kernel (in crosses involving Hybrid 128), hairy neck, length of kernel, fertility, development of kernel, height of culm, and length of spike. Fertility was determined as percentage calculated from the number of kernels produced in a given number of florets, or as the average number of kernels per spikelet, usually

calculated from two spikes per plant. To obtain the average length of kernel, 10 average kernels from each plant were laid end to end in a narrow crease in a flat board and measured.

FIRST-GENERATION WHEAT × RYE CROSSES IN 1924

Hybrid 128 and Kanred wheats, Red Winter spelt, Clackamas and Peliss wheats, Black Winter emmer, and Polish wheat were crossed with Rosen and Dakold ryes. (Table 1.) Crosses were obtained readily with varieties of the 42-chromosome wheats. None was obtained with Black Winter emmer and very few with Polish, Peliss, and Clackamas wheats. Crossed kernels were more or less shriveled or misshapen in many cases. Kernels from Hybrid 128 and Kanred ranged from fairly plump to shriveled. In Hybrid 128 there were a number of very small kernels.

TABLE 1.—*Wheat × rye crosses made at University Farm, Davis, Calif., 1924 and 1926*

Year and cross	Chromosome group of wheat parent	Spikes used	Florets crossed	Kernels obtained	Florets setting seed
1924	*Number*	*Number*	*Number*	*Number*	*Per cent*
Red Winter×Rosen	42	4	96	[a] 17	17.7
Red Winter×Dakold	42	4	96	[a] 24	25.0
Hybrid 128×Rosen	42	4	96	[b] 70	72.9
Hybrid 128×Dakold	42	4	96	[b] 81	84.4
Kanred×Rosen	42	4	96	[a] 30	31.3
Kanred×Dakold	42	4	96	[a] 57	59.4
Peliss×Rosen	28	4	96	[c] 2	2.1
Peliss×Dakold	28	4	96	2	2.1
Black Winter×Rosen	28	4	96	0	0
Black Winter×Dakold	28	4	96	0	0
Polish×Rosen	28	3	72	0	0
Polish×Dakold	28	3	72	[a] 2	2.8
Clackamas×Rosen	28	3	72	[c] 2	2.8
Clackamas×Dakold	28	3	72	[c] 8	11.1
1926					
Hybrid 128×Rosen	42	2	54	23	42.7
Red Winter×Rosen	42	2	48	3	6.3
Kanred×Rosen	42	2	50	3	6

[a] Fairly well developed.
[b] Fairly well developed but small.
[c] Badly shriveled.

Observations and measurements were made on height of plant, type of spike, length of main spike, hairy neck, length of beak, and color of straw. Most of these characters were intermediate or inclined to one or the other parent. Height of plant was inclined strongly to that of the rye parent. The spike in the F_1 hybrid of crosses with Hybrid 128 wheat is a long-club type. (Fig. 2, B.) The length of spike in Red Winter spelt×Dakold rye exceeded that of the parents. Hairy neck was heavy on most plants, but it was absent on a few. This variation in F_1 probably is due to the fact that a small percentage of Rosen plants were glabrous. Length of beak of the outer glume, considered a very constant character in wheat, was distinctly wheatlike. At Davis, the F_1 hybrid and the rye parents both had purple straw, and the wheat parents had white straw. The coleoptiles and leaf sheaths of F_1 seedlings were reddish purple like those of the rye parents. (Table 2.)

At blossoming time the glumes opened, permitting the anthers to extrude. The glumes have a tendency to remain open for a consid-

FIGURE 2.—Parents and F_1 hybrid of Hybrid 128 wheat × Rosen rye. A, Rosen; B, F_1 hybrid; C, Hybrid 128. (Two-thirds natural size)

erable time. No anthers were observed to shed their pollen. On several occasions anthers were collected for pollen examination. Only a few abnormal pollen grains of variable size were found.

TABLE 2.—*Description of F_1 plant characters in wheat × rye crosses, 1925*

Cross or parent	Plants	Height of plants	Type of spike	Length of main spike	Hairy neck	Length of beak	Color of straw
	Number	*Inches*		*Cm.*	*Degree*	*Mm.*	
Red Winter × Dakold	2	53–60	Lax, speltlike	14 –16	Heavy	0.5– 1	Purple.
Hybrid 128 × Dakold	6	53–54	Compact, long club.	7.5– 9	3 light at top; 3 none.	.5– 1	Do.
Hybrid 128 × Rosen	5	50–60	do	6 – 7	4 heavy; 1 light	.5– 1	Do.
Kanred × Rosen	3	55–58	Lax	12 –13	1 medium heavy; 2 none.	5 –10	Do.
Kanred × Dakold	3	56–61	do	14 –15.5	Medium heavy	5 –15	Do.
Hybrid 128	10	43–52	Compact, club	4.5– 5.5	None	.5	White.
Kanred	10	47–52	Lax	8.5–10	do	3 – 8	Do.
Rosen	5	58–65	Long, lax	12 –18	2 medium heavy; 3 light.		Purple.

EFFECT OF BAGGING ON FERTILITY OF F_1 HYBRIDS AND WHEAT PARENTS

The effect of isolation on the fertility of the F_1 plants was studied. Seventy-seven heads containing 4,245 florets were covered individually with glassine bags a short time before flowering. All heads were completely sterile. Nineteen heads on five crosses not covered yielded kernels only in the two crosses involving Hybrid 128. From 11 F_1 heads, containing 1,334 florets of the crosses with Hybrid 128, 8 kernels were obtained, equaling 0.6 per cent, or 6 kernels per 1,000 flowers. (Table 3.)

TABLE 3.—*Relative fertility of F_1 wheat × rye hybrids when bagged and when not bagged, 1925*

Cross	Bagged				Not bagged			
	Heads	Florets	Kernels obtained	Fertility	Heads	Florets	Kernels obtained	Fertility
	Number	*Number*	*Number*	*Per cent*	*Number*	*Number*	*Number*	*Per cent*
Red Winter × Dakold	13	743	0	0	2	170	0	0
Hybrid 128 × Dakold	18	950	0	0	6	694	6	.86
Hybrid 128 × Rosen	15	866	0	0	5	640	2	.31
Kanred × Rosen	14	746	0	0	3	328	0	0
Kanred × Dakold	17	940	0	0	3	360	0	0

A number of heads of Dakold and Rosen rye also were covered with glassine bags. The fertility of Dakold was 1.6 per cent and that of Rosen 5.4 per cent. Although a high degree of self-sterility is normal in rye, the high temperature and low humidity during the blooming period no doubt increased the sterility in the covered heads.

The effect of bagging on fertility in Hybrid 128 and Kanred wheats was studied in 1928. The average number of kernels per spikelet in bagged Hybrid 128 was 1.79, and in unbagged, 2.18; in bagged Kanred, 1.64, and in unbagged, 1.92. The average reduction in length of kernel from bagging in Hybrid 128 was 0.2 mm., and in Kanred, 0.3 mm. Bagging increased the number of rudimentary spikelets 2.7 per cent in Hybrid 128, but decreased them 1.9 per cent in Kanred. (Not shown in Table 4.) Bagging individual plants reduced the fertility 17.9 per cent in Hybrid 128 and 15.0 per cent in Kanred. (Table 4.)

TABLE 4.—*Relative fertility of wheat varieties when bagged and when not bagged, 1928*

Variety	Plants	Heads	Spikelets	Total kernels	Average kernels per spikelet	Average length of kernel	Reduction in fertility
	Number	*Number*	*Number*	*Number*	*Number*	*Mm.*	*Per cent*
Hybrid 128 [a]	10	19	402	719	1.79	5.5	17.9
Hybrid 128 [b]	10	20	444	969	2.18	5.7	
Kanred [a]	10	20	358	587	1.64	6.3	15.0
Kanred [b]	10	20	347	667	1.92	6.6	

[a] Individual plants bagged. [b] Not bagged.

In Rosen rye a higher degree of sterility occurred in individually bagged heads than in individually bagged plants.

THE FIRST BACK CROSS

FIRST-GENERATION PLANTS, 1925

Since the wheat × rye F_1 generation is completely self-sterile, it is necessary to back-cross with pollen from one parent or the other in order to obtain fertilization. Wheat pollen only was used in these experiments. For all back crosses in 1925, 49 heads, containing 2,228 florets, were pollinated, and 39 kernels were obtained. Fertility percentages were 1.2 and 1.3 in Hybrid 128 back crosses, and 1.5 and 2.6 in Kanred back crosses. (Table 5.) From the open-pollinated F_1 Hybrid 128 wheat × rye plants, 0.86 and 0.31 per cent kernels were obtained. (Table 3.)

TABLE 5.—*Number of kernels obtained in back-crossing (wheat × rye) × wheat, 1925*

Cross	Heads crossed	Florets pollinated	Kernels obtained	Fertile florets	Average kernels per spikelet
	Number	*Number*	*Number*	*Per cent*	*Number*
(Hybrid 128×Dakold)×Hybrid 128	12	434	5	1.2	0.024
(Hybrid 128×Rosen)×Hybrid 128	10	452	6	1.3	.026
(Kanred×Dakold)×Kanred	12	606	9	1.5	.030
(Kanred×Rosen)×Kanred	15	736	19	2.6	.052

FIRST-GENERATION PLANTS (WR_1W_1),[6] 1926

The characters of the back-crossed progeny of three hybrids, Hybrid 128 × Rosen, Kanred × Dakold, and Kanred × Rosen, obtained by back crossing on the F_1 with the wheat parent, were studied.

[6] The designation WR_1W_1 used throughout this paper denotes that the F_1 of the wheat × rye cross (written as WR_1) has been back crossed with the wheat parent W, resulting in the plant or series of plants in question. The formula without the subscript, or generation numeral, as WR_1W, refers to the crossed kernels, or P_1, of the back cross in question. The generation of the back cross is designated by the usual subscript numeral, as WR_1W_1, WR_1W_2, etc. WR_1W_2 indicates that the plant WR_1W_1 has been selfed, producing a second generation. Likewise, $WR_1W_1W_1$ indicates that the original F_1 hybrid has been back crossed with wheat and the resulting hybrid again back crossed with the wheat parent, producing the plant thus designated. When this plant is selfed the resulting plant is indicated by $WR_1W_1W_2$, and later selfed generations by the usual subscript numerals 3, 4, etc. In crosses involving unequal chromosomes, or chromosomes which do not pair, plants from the back cross on F_1 usually vary somewhat in type, unlike the F_1 plants of ordinary crosses, on account of variability in constitution of the gametes of the hybrid.

Twenty-five back-crossed plants in addition to parents were grown in 1926. These plants too were more wheatlike than those in the F_1

FIGURE 3.—Back-crossed first-generation hybrids and parents of Hybrid 128 wheat × rye. A, Hybrid 128 wheat × Rosen rye; B, Hybrid 128 wheat × Dakold rye; A, *a*, and B, *a*, F_1 hybrid parents; A, *c*, and B, *c*, Hybrid 128; A, *b*, *c*, *d*, and B, *b*, *c*, *d*, WR_1W_1 hybrid heads. Note variation in WR_1W_1 heads due to variable constitution of ovules

generation, but rye characters persisted. Segregation into several different types occurred, which showed that there must have been differences in constitution of the F_1 gametes. (Fig. 3 and Table 6.)

TABLE 6.—*Characters of first back-cross first-generation (wheat × rye) × wheat hybrids, 1926*

Cross, parent, and cross No.	Plant characters					Kernel characters		
	Length of main spike	Hairy neck	Fertility			Color	Average length	Development
			Florets	Kernels obtained				
	Cm.	*Degree*	*Number*	*Number*	*Per cent*		*Mm.*	
Hybrid 128 × Rosen: [a,b]								
42A1	8	Light	88	10	11.4	Red	6.9	Slightly shriveled.
42B1	5.5	None	84	0				
42C1	5.5	....do	94	2	2.1	Red	6	One kernel shriveled.
Kanred × Dakold: [a,b]								
43A1	11	Medium heavy	74	0				
43B1	6	Light at top	50	0				
43B2	9	....do	62	0				
43C1	9.5	....do	68	13	19.1	Red pale	7.1	Medium plump.
43D1	9.5	None	76	0				
43D2	8	Light	34	0				
43D3	8.5	Medium heavy		0				
Kanred × Rosen: [a,b]								
44A1		None	34	0				
44B1		....do	56	3	5.4	Red pale	5.7	Plump.
44B2		....do		0				
44C1		....do	72	0				
44C2		....do	62	0				
44D1	14.5	Light	82	3	3.7	Red	7.3	Badly shriveled.
44E1		Medium heavy		0				
44F1		None		0				
44F2		....do		0				
44G1 [c]	16	Very light	98	4	4.1	Red	6.8	Slightly shriveled.
44A2 [c]	15	Light	84	2	2.4	....do	7	Badly shriveled.
44C3 [c]	11	None	78	4	5.1	Red pale	7.5	Slightly shriveled.
44D2 [c]	11	Medium heavy	78	0				
44E2 [c]		None	64	5	7.8	Red pale	7	Do.
44F3 [c]	12	....do	76	12	15.8	....do	8.2	Medium plump.
Dakold	11	Very heavy	128	9	7	Red	6.4	Badly shriveled.
Rosen	15	Heavy	160	55	34.4	Gray, few light red.	6.5	Medium but shorter than normal.
Kanred [c,d]	10	None	[f] 283	672	[g] 2.37	Red	6.9	Plump.
Hybrid 128 [c,e]	5	....do	[f] 71	124	[g] 1.75	White	5.1	Badly shriveled.

[a] Parent wheat varieties were used in back crossing on F_1 in all cases. Heads of (Hybrid 128 × Rosen) × Hybrid 128 long-club type in plant 42A1; others short club. All heads lax in Kanred × rye × Kanred crosses.
[b] Plants bagged.
[c] Plants not bagged.
[d] Average of 10 plants.
[e] Average of 2 plants.
[f] Number of spikelets.
[g] Kernels per spikelet.

All back crosses segregated for hairy neck. The expression of hairy neck varied from very light at the top of the peduncle to medium and heavy. Of 3 Hybrid 128 wheat × Rosen rye back-crossed plants, 1 had light hairy neck and 2 had none; of the Kanred wheat × Dakold rye back-crossed plants, 6 had medium and light hairy neck and 1 had none; and of the Kanred wheat × Rosen rye back-crossed plants, 5 had medium and light hairy neck and 10 had none. Two plants of the Hybrid 128 wheat × Rosen rye back cross produced red kernels; the third plant was sterile.

The type of head varied mainly in size and length (column 5, Table 2), but almost exact parental duplicates were represented. Similarly, length of kernel varied from shorter than that of the short-kerneled parent to longer than that of Rosen. Fifteen of the selfed plants were sterile. The fertility of the remainder was variable up to about 19 per cent. Seed from 3 of the 10 plants producing kernels was well developed, while that from the remainder was more or less badly shriveled.

THE SECOND BACK CROSS

Relative Fertility from Crossing and Selfing

In order to get strains of wheatlike material possessing rye characters as soon as possible—for example, hairy neck on a wheatlike plant—the back-cross progeny plants were again back crossed with their respective wheat parents. Seventeen plants were back crossed. Data on the fertility of these plants, when back crossed the second time and when selfed, are given in Table 7. In most cases a higher set of seed was obtained from back-crossed plants than from selfed plants. Plump kernels were obtained in several plants. On back crossing, a lower set of seed, with more shriveled kernels, was obtained from the apparently self-sterile plants than from the partly self-fertile plants. Fifty-eight heads containing 1,779 florets were emasculated and pollinated, and 323 kernels were obtained. The average fertility was 18.2 per cent.

Table 7.—*Relative fertility of selfed and back-crossed first-generation (wheat × rye) × wheat hybrids, 1926*

Cross and No.	Parent plants back crossed					Parent plants selfed (bagged)				
	Heads crossed	Florets pollinated	Kernels			Heads examined	Florets	Kernels		
			Obtained	Condition	Seed set			Obtained	Condition	Seed set
Hybrid 128×Rosen:	No.	No.	No.		P. ct.	No.	No.	No.		P. ct.
42A1×Hybrid 128	3	100	38	Plump and shriveled.	38.0	2	88	10	Slightly shriveled.	11.4
42B1×Hybrid 128	5	144	4	Badly shriveled	2.8	2	84	0		
42C1×Hybrid 128	7	260	12	Plump	4.6	2	94	2	1 shriveled; 1 plump.	2.1
Kanred×Dakold:										
43A1×Kanred	3	96	3	do	3.1	2	74	0		
43B1×Kanred	3	94	27	do	28.8	2	50	0		
43B2×Kanred	5	129	20	Plump, some shriveled.	15.5	2	62	0		
43C1×Kanred	2	52	28	Plump	53.8	2	68	13	Medium plump	19.1
43D1×Kanred	3	98	15	Shriveled	15.3	2	76	0		
43D2×Kanred	2	56	2	Plump	3.6	1	34	0		
43D3×Kanred	5	159	17	do	10.7			0		
Kanred×Rosen:										
44A1×Kanred	2	74	7	Medium plump	9.5	1	34	0		
44B1×Kanred	3	92	73	Plump	79.4	2	56	3	Shriveled	5.4
44B2×Kanred	3	78	4	Medium plump	5.1			0		
44C1×Kanred	2	58	0			2	72	0		
44C2×Kanred	2	52	0			2	62	0		
44D1×Kanred	3	83	16	Shriveled	19.2	2	82	3	Badly shriveled	3.7
44G1×Kanred	5	154	57	Plump	37	2	98	4	Slightly shriveled	4.1

First-generation Plants, 1927

As a result of the second back cross, there were grown of the Hybrid 128×Rosen combination 2 families consisting of 13 individuals; of Kanred×Dakold, 5 families, of 16 individuals; and of Kanred×Rosen, 4 families, of 22 individuals. As a result of selfing the plants of the first back-crossed generation, WR_1W_1, one family of each of the first two crosses and two of the third were grown, producing 6, 12, and 22 plants, respectively. Table 8 presents a summary of the data obtained on 11 $WR_1W_1W_1$ families, 4 WR_1W_2 families, and the two wheat parents.

TABLE 8.—*Segregation for hairy neck, kernel color, fertility, kernel length, and kernel development in wheat × rye back-crossed families, 1927*

Cross, generation, and parent	Plant ancestor	Family	Total plants	Sterile plants	Plants with hairy neck of indicated degree			Plants with kernels of indicated color		Fertility		Kernel length	Plants with greater kernel length than wheat parent	Plants with indicated kernel development			
					Heavy and medium	Light	None	Red	White	Average of kernels per spikelet	Plants with fewer kernels than wheat parent			Plump and medium	Slightly shriveled	Badly shriveled	
Hybrid 128×Rosen:																	
		No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
WR_1W_1	42A1					1		11		0.23		6.9			1		
$WR_1W_1W_1$		98B	11		3		8	4	7	.02–.81	11	5.6–8.2	6	6	2	3	
WR_1W_1	42C1						1	1		.04		6.0			1		
$WR_1W_1W_1$		98Bd	2				2	1	1	.97–1.00	2	6.0–6.9	1		2		
WR_1W_2	[a] 42A1		6	1	2	1	4	4	1	.62–1.43	6	6.7–8.1	1	5		1	
Hybrid 128			4				4		4	1.42–1.86		5.8–6.3		3		1	
Kanred×Dakold:																	
WR_1W_1	43A1				1			1									
$WR_1W_1W_1$		99B	1		1			1		.04	1	7.0	1	1			
WR_1W_1	43B1					1		1									
$WR_1W_1W_1$		99Ba	3	2	1		2	1		.34	3	6.1	1			1	
WR_1W_1	42B2					[b] 1		1									
$WR_1W_1W_1$		99Cb	1	1			1			0							
WR_1W_1	43C1					1		1		.38		7.1		1			
$WR_1W_1W_1$		99Ac	9		1		8	9		.56–1.68	9	6.6–7.5	2	6	1	2	
WR_1W_1	43D3				1			1									
$WR_1W_1W_1$		99Cf	2		1		1	2		.05–.97	2	5.7–7.0	1	1		1	
WR_1W_2	43C1		12	3		3	9	9		.45–1.78	1	6.7–8.3	2	5	4		
Kanred×Rosen:																	
WR_1W_1	44B1						1	1		.11		5.7		1			
$WR_1W_1W_1$		400Aa	13				13	13		.66–1.87	8	6.3–7.5	6	11	1	1	
WR_1W_1	44B2						1	1									
$WR_1W_1W_1$		400Cb	1				1			0							
WR_1W_1	44D					1		1		.07		7.3				1	
$WR_1W_1W_1$		400Ce	3				3	3		.49–1.44	3	6.6–7.7	1	2		1	
WR_1W_1	44G					[b] 1		1		.08		6.8			1		
$WR_1W_1W_1$		400Dd	5	1			5	4		0–1.06	5	7.0–7.9	4	2		2	
WR_1W_1	44A2					[b] 1		1		.05		7.0				1	
WR_1W_2		44A2	10			2	8	8		.61–1.92	6		1	3	4	3	
WR_1W_1	44G1					[b] 1		1		.08		6.8			1		
WR_1W_2		44G1	12			2	10	12		.01–1.18	12	6.2–8.5	6	4	6	2	
Kanred			4				4	4		1.51–1.91		6.7–6.9		4			

[a] On one plant in this family no data on kernel color were recorded.
[b] At top of peduncle.

In these second back-crossed families there was segregation for hairy neck, color of kernel, length of spike and kernel, and fertility. Similar segregation occurred in the WR_1W_2 generation. Variation in length of spike in these generations is shown in Figures 4 and 5. Hairy-necked plants were always fewer in number than glabrous-necked plants, and red-kerneled plants were always fewer in number than white-kerneled plants. This relation was true likewise of long-spiked and long-kerneled plants, and their respective allelomorphs.

The fertility of all plants in nine families was below the minimum recorded for the respective parent plants. In one Kanred×Dakold WR_1W_2 family of 12 plants (43C1), only one plant was below the parent minimum. Evidently this family had reverted almost completely to the wheat-parent type. Segregation for hairy neck and length of kernel was still occurring. Length of spike was within the

range of the Kanred parent, but height of plant was below that of the parent, probably as a result of bagging. Nearly all families

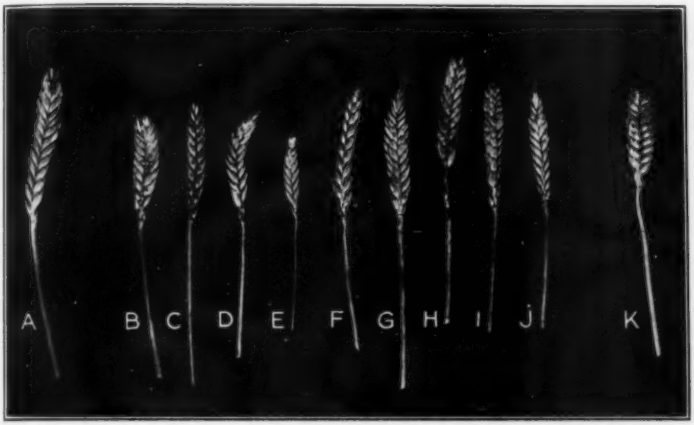

FIGURE 4.—Second back-cross first-generation hybrids and parents. A, WR_1W_1 (same as fig. 3, A, *b*); B–J, head types resulting from the second back cross; K, Hybrid 128 wheat. Note variability resulting when plant with head type such as A is used for back crossing

FIGURE 5.—Parents, first back-cross first-generation hybrid, and selfed first back-cross first-generation hybrids of Hybrid 128 wheat × Rosen rye back crosses: A, F_1 hybrid; B, WR_1W_1 (same as fig. 3, A, *b*); C, Hybrid 128 wheat; D–H, WR_1W_2 population. Note type of variation when selfed

contained plants with length of kernel more than that of the parental maximum.

An interesting segregant (fig. 6, C) appeared in the $WR_1W_1W_1$ generation of Hybrid 128×Rosen family 98Bd. This family consisted of two plants, one of which seemed to be identical with plants of Hybrid 128 except that it had angular red kernels. The other plant was slightly larger with slightly longer white kernels. (Fig. 6, B.)

Most families had plants with more or less badly shriveled kernels. Endosperm development has been found to parallel closely the chromosome content of the fusion nucleus. The cytologic relationships are discussed in another paper by the author (*5*).

SECOND BACK-CROSS SECOND-GENERATION AND FIRST BACK-CROSS THIRD-GENERATION PLANTS, 1928

Seed was selected from plants having rye characters and from plants without apparent rye characters in order to get true-breeding strains and to recover parental types. In each case plants of comparatively high fertility were used.

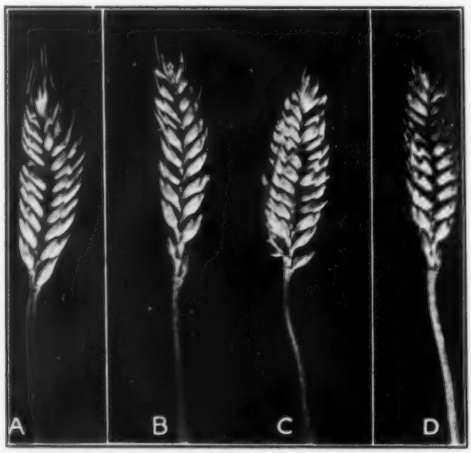

FIGURE 6.—Second back-cross second-generation hybrids and parents. A, WR_1W_1 parent head (same as fig. 3, A, *c*); B and C, wheatlike heads of hybrid plants from the second back cross, $WR_1W_1W_1$; D, Hybrid 128 wheat. Seed from the same plant as C, as the result of selfing, produced white-kerneled and red-kerneled plants; white-kerneled plants were identical with Hybrid 128. Selfed seed from the same plant as B, although white kerneled, produced hairy-necked and nonhairy-necked plants

In 1928 6 families of the Hybrid 128 × Rosen combination, 3 of the Kanred×Dakold, and 6 of the Kanred× Rosen were grown in the $WR_1W_1W_2$ generation; and 1, 2, and 3 families, respectively, of the same combinations were grown in the WR_1W_3 generation. A total of 941 hybrid plants and 80 parent plants was studied.

The results from 10 hybrid families, and single families from each of the 2 wheat parents are presented in Table 9.

Two families each of the Kanred×Dakold and Kanred×Rosen crosses, both in the $WR_1W_1W_2$ generation, had regained the fertility of the wheat parent. The range of length of spike of all was nearly identical with that of the parental range, and none had hairy neck. In all four families the maximum length of kernel was more than that of the parental maximum, however, showing that rye influence still remained. The percentage of long-kerneled plants (average length of kernel 6.9 mm. or more) in these families ranged from 17.9 to 56.5. A minority of plants with the rye character was found, except in one family. No true-breeding hairy-necked families occurred in either of these families nor in the Hybrid 128×Rosen back cross. Nor were any true-breeding red-kerneled families found in the latter.

TABLE 9.—*Segregation for hairy neck, kernel color, fertility, kernel length, and kernel development in wheat × rye back-crossed families, 1928*

Cross, generation, and parent	Plant ancestor, number	Family number	Total plants	Sterile plants	Plants with hairy neck of indicated degree			Plants with kernels of indicated color		Fertility		Kernel length	Plants with greater kernel length than wheat parent	Plants with indicated kernel development		
					Heavy and medium	Light	None	Red	White	Average of kernels per spikelet	Plants with fewer kernels than wheat parent			Plump and medium	Slightly shriveled	Badly shriveled
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*Mm.*	*No.*	*No.*	*No.*	*No.*
Hybrid 128×Rosen																
WR_1W_1	42A1					1		1		0.23		6.9			1	
$WR_1W_1W_1$	98B4				1			[a] 1		.63		8.2		1		
$WR_1W_1W_2$		98B4	[b] 20	2	8		10	4	13	0-2.18	12	5.0-7.4	11	8	2	8
WR_1W_1	42C1						1	1		.04		6.0			1	
$WR_1W_1W_1$	983B3						1	1		.97		6.0		1		
$WR_1W_1W_2$		98Bd3	114				114	32	82	.12-1.88	63	5.1-6.4	15	68	26	20
WR_1W_1	42C1						1	1		.04		6.0			1	
$WR_1W_1W_1$	98Bd4						1		1	1.00		6.9		1		
$WR_1W_1W_2$		98Bd4	60	2	5	11	44		58	0-1.52	50	5.1-7.0	24	29	10	19
WR_1W_1	42A1					1		[c] 1		.23		6.9			1	
WR_1W_2	42A1-1				1			[c] 1		1.27				1		
WR_1W_2		42A1-1	58	2	21	4	33	19	37	0-2.40	21	5.8-7.7	54	40	3	13
Hybrid 128 anred×Dakold:			30				30		30	1.42-2.77		5.2-5.9		30		
WR_1W_1	43C1					1		1		.38		7.1		1		
$WR_1W_1W_1$	99Ac1						1	1		1.16		6.7		1		
$WR_1W_1W_2$		99Ac1	67				67	67		1.43-2.54	0	5.9-7.5	39	65	1	1
WR_1W_1	43C1					1		1		.38		7.1		1		
$WR_1W_1W_1$	99Ac7				1			1		1.33		7.5		1		
$WR_1W_1W_2$		99Ac7	48		5	7	36	48		.14-1.86	20	5.7-7.9	21	35	11	2
WR_1W_1	43C1					1		1		.38		7.1		1		
$WR_1W_1W_1$	99Ac8						1	1		1.56		7.0		1		
$WR_1W_1W_2$		99Ac8	56				56	56		1.35-2.75	0	5.5-7.3	22	51	4	1
Kanred×Rosen:																
WR_1W_1	44B1						1	1		.11		5.7		1		
$WR_1W_1W_1$	400Aa1						1	1		1.66		6.3		1		
$WR_1W_1W_2$		400Aa1	64				64	64		1.34-2.47	0	5.8-7.1	12	55	8	1
WR_1W_1	44B1						1	1		.11		5.7		1		
$WR_1W_1W_1$	400Aa5						1	1		1.38		7.0		1		
$WR_1W_1W_2$		400Aa5	62				62	62		1.38-2.67	0	6.0-7.2	17	52	7	3
WR_1W_1	44D					1		1		.07		7.3				1
$WR_1W_1W_1$	400Ce1						1	1		1.38		7.7		1		
$WR_1W_1W_2$		400Ce1	[d] 55	1			54	54		0-2.78	12	6.7-7.5	28	38	8	7
Kanred			35				35	35		1.23-2.50		6.0-6.7		34		1

[a] Dull white.
[b] Including two grassy dwarfs.
[c] Pale red.
[d] Including one grassy dwarf.

The progeny of the red-kerneled plant of the Hybrid 128×Rosen $WR_1W_1W_1$ family, 98Bd3, did not breed true for kernel color, but from all indications this plant was homozygous except for this character. (Fig. 7.) Out of 114 plants, 32 were red kerneled and 82 white kerneled, a ratio of 1 red to 2.56 white. Seventy-eight per cent of the red-kerneled plants and 46.3 per cent of the white-kerneled plants were below the parental minimum of fertility. There was a definite tendency for red-kerneled plants to have longer kernels than the white-kerneled plants. The family of the white-kerneled sib of the red-kerneled plant 98Bd4 (fig. 6, B) bred true for white kernel but segregated for all other characters studied.

Segregating families produced a larger number of plants with shriveled kernels than did parental-type families.

RYE CHARACTERS AND FERTILITY IN SECOND BACK-CROSS THIRD-GENERATION AND FIRST BACK-CROSS FOURTH-GENERATION PLANTS, 1929

An effort was made to get true-breeding wheat types having one or more of the rye characters—hairy neck, red kernel color, long kernel, and winter hardiness. Fifteen Hybrid 128×Rosen, five Kanred×Dakold, and four Kanred×Rosen families were grown in the $WR_1W_1W_3$ generation. Seven Hybrid 128×Rosen and two Kanred×Dakold families were grown in the WR_1W_4 generation. There were 2,193 hybrid and 119 parent plants harvested and studied in 1929.

Data on 19 families, together with similar data for ancestral plants and parent varieties, are presented in Table 10. One family, 98B4–2, bred true for hairy neck, and one, 42A1–1–37, bred nearly true for red kernel. Both were Hybrid 128×Rosen back crosses, the first a $WR_1W_1W_3$ and the second a WR_1W_4.

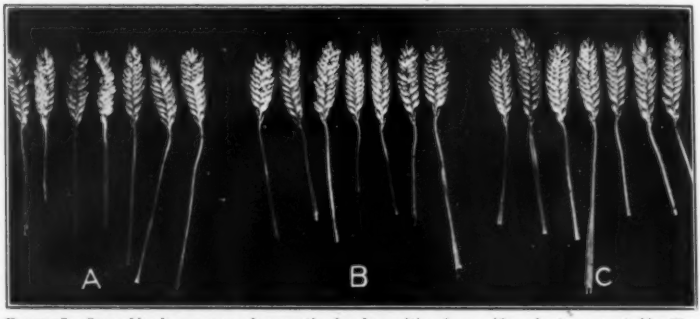

FIGURE 7.—Second back-cross second-generation heads resulting from selfing plant represented by Figure 6, C, and heads of Hybrid 128 wheat for comparison. A, Hybrid 128 wheat; B, white-kerneled segregates; C, red-kerneled segregates. Note close similarity of segregates B and C to Hybrid 128

The hairy-necked family originated from a plant with unusually heavy pubescence extending down the peduncle about 2 inches below the spike. The other three characters, fertility, color, and length of kernel, were segregating in this family. Twenty plants were below the parental minimum of fertility, and one plant, a semidwarf, was sterile.

Family 42A1–1–37, nearly true breeding for red kernels, originated from a red-kerneled line of ancestors. Other characters besides kernel color were segregating in this family. Twenty-one of 53 plants were sterile, 1 being a semidwarf. One of the 32 fertile plants was white kerneled. It seems likely that this plant was not a mechanical mixture, but resulted from the elimination of the rye factor or factors responsible for red color.

Ten red-kerneled plants from the $WR_1W_1W_2$ Hybrid 128×Rosen family, 98Bd3, which was segregating for kernel color but otherwise true breeding, were grown. Not one true-breeding red-kerneled family resulted. In nine families there was a preponderance of white-kerneled plants as usual, but in one family, Bd3–19, there were 22 red to 14 white. The most fertile red-kerneled plants were chosen as parents for these 10 families. It is possible that true-breeding plants were unconsciously eliminated. The kernels of the red-kerneled plants were fairly well developed in most cases, although more or less angular; the kernels of the white-kerneled plants were mostly plump and well filled.

TABLE 10.—*Segregation for hairy neck, kernel color, fertility, kernel length, and kernel development in wheat × rye back-crossed families, 1929*

Cross, generation, and parent	Plant ancestor number	Family number	Total plants	Sterile plants	Dwarf plants	Plants with hairy neck of indicated degree			Plants with kernels of indicated color [a]		Fertility		Kernel length	Plants with greater kernel length than wheat parent	Plants with indicated kernel development		
						Heavy and medium	Light	None	Red	White	Average of kernels per spikelet	Plants with fewer kernels than wheat parent			Plump and medium	Slightly shriveled	Badly shriveled
Hybrid 128 × Rosen:																	
WR_1W_1	42A1						1		1		0.23		6.9			1	
$WR_1W_1W_1$	98B4					1				[b] 1	.63		8.2		1		
$WR_1W_1W_2$	98B4–2					[c] 1			1		.25		7.4				1
$WR_1W_1W_3$		[d]	30	1	1	24	6		[e] 4	25	0–2.76	20	5.7–7.7	26	28		1
WR_1W_1	42C1							1			.04		6.0				1
$WR_1W_1W_1$	98Bd3							1			.97		6.0		1		
$WR_1W_1W_2$	98Bd3–4							1			1.32		6.2		1		
$WR_1W_1W_3$		[d]	72					72	8	32	1.63–2.50	2	5.5–6.6	3	40		
$WR_1W_1W_2$	98Bd3–16							1	1		1.45		6.0		1		
$WR_1W_1W_3$		[d]	67					67	7	28	1.22–2.40	8	5.2–6.1		35	1	
$WR_1W_1W_2$	98Bd3–19							1	1		.84		6.0			1	
$WR_1W_1W_3$		[d]	36					36	22	14	1.16–2.35	11	5.4–6.2		36		
$WR_1W_1W_2$	98Bd3–25							1	1		1.35		6.1		1		
$WR_1W_1W_3$		[d]	66					66	14	18	.72–2.77	11	5.5–6.5	1	32		
$WR_1W_1W_2$	98Bd3–20							1	1		1.62		5.8			1	
$WR_1W_1W_3$		[d]	61					61	7	14	1.63–2.63	2	5.5–6.2		20	1	
$WR_1W_1W_2$	98Bd3–36							1	1		1.09		5.7		1		
$WR_1W_1W_3$		[d]	75					75	6	14	1.48–2.62	3	5.6–6.3	2	19		1
$WR_1W_1W_2$	98Bd3–44							1	1		1.23		5.5		1		
$WR_1W_1W_3$		[d]	70					70	7	12	.58–2.5	5	4.1–6.0		17		2
$WR_1W_1W_2$	98Bd3–59							1	1		1.39		5.8		1		
$WR_1W_1W_3$		[d]	68					68	6	14	1.36–2.44	4	4.4–6.3	2	19		1
$WR_1W_1W_2$	98Bd3–76							1	1		1.52		5.6		1		
$WR_1W_1W_3$		[d]	80					80	8	12	1.66–2.19	2	5.4–6.1		20		
$WR_1W_1W_2$	98Bd3–103							1	1		1.50		5.4		1		
$WR_1W_1W_3$		[d]	77					77	4	16	1.57–2.80	3	5.3–6.3	1	19		1
$WR_1W_1W_3$	98Bd3	[e]	264					264	90	174	.58–2.77	53	4.1–6.6	9	256	3	5
Hybrid 128			80					80		41	1.80–2.70		5.6–6.2		37		4
WR_1W_1	42A1						1		1		.23		6.9			1	
WR_1W_2	42A1–1					1			1		1.27				1		
WR_1W_3	42A1–1–1					1			[f] 1		1.17		7.0		1		
WR_1W_4		[g]	55	2		14	9	32	19	19	0–2.53	22	5.0–7.4	31	16	18	4
WR_1W_3	42A1–1–23					1				1 2	2.12		6.6		1		
WR_1W_4		[g]	39			4	5	30		37	1.37–2.67	13	5.5–7.1	15	25	4	8
WR_1W_3	42A1–1–37					1			1		1.48		7.4		1		
WR_1W_4		[g]	52	21	1	2	20	29	30	1	0–2.07	49	4.7–7.4	33	9	10	12
Kanred × Dakold:																	
WR_1W_1	43C1						1		1		.38		7.1		1		
$WR_1W_1W_1$	99Ac7					1			1		1.33		7.5		1		
$WR_1W_1W_2$	99Ac7–18					1			1		1.86		7.0		1		
$WR_1W_1W_3$		[d]	66				1	35	36		1.00–3.43	2	6.1–7.5	3	35		1
$WR_1W_1W_1$	99Ac3							1	1		1.56		7.0		1		
$WR_1W_1W_2$	99Ac8–23							1	1		1.98		7.3		1		
$WR_1W_1W_3$		[d]	88		4			84	43		1.23–3.25	15	5.7–7.2	1	41	2	
Kanred			77					44	44		1.72–2.51		6.2–7.2		41		3
Kanred × Rosen:																	
WR_1W_1	44B1								1	1	.11		5.7				1
$WR_1W_1W_1$	400Aa13								1	1	.92		7.0		1		
$WR_1W_1W_2$	400Aa13–36								1	1	1.72		7.2		1		
$WR_1W_1W_3$		[d]	37					37	37		1.26–2.35	10	5.9–7.3	2	32		5
WR_1W_1	44D						1		1		.07		7.3				1
$WR_1W_1W_1$	400Cc1							1	1		1.38		7.7		1		
$WR_1W_1W_2$	400Cc1–3							1	1		1.94		7.3		1		
$WR_1W_1W_3$		[d]	71		1			70	34		.28–2.46	8	5.6–7.5	2	32		2
$WR_1W_1W_2$	400Cc1–7							1	1		1.67		7.2		1		
$WR_1W_1W_3$		[d]	56		2			53	33		1.41–2.43	5	6.8–7.8	18	33		

[a] Kernel color, fertility, kernel length, and kernel development were determined on approximately 20 plants in each family in ($WR_1W_1W_0$) F_1.

[b] Dirty white.

[c] Very heavy.

[d] Cross number same as F_2 family.

[e] Total plants of all F_2 families of 98Bd3

[f] Dull red.

[g] Cross number same as F_2 family.

In 1929, parent varieties and parental strains generally produced plump, well-filled grain, but segregating families produced about the usual proportion of shriveled kernels.

RELATIONSHIP OF FERTILITY AND KERNEL LENGTH IN SECOND BACK-CROSS SECOND AND THIRD GENERATION FAMILIES AND FIRST BACK-CROSS THIRD-GENERATION FAMILIES, 1928 AND 1929

WHEATLIKE FAMILIES WITH RYE CHARACTERS

Although no wheatlike strain having true-breeding rye characters has been obtained so far as can be determined, the isolation of strains apparently with a single rye character, as well as others with two or more rye characters, affords opportunity to study the effect of the rye complement on fertility and length of kernel in the wheat plant. Table 11 presents data showing some of these relationships.

In 1927, the red-kerneled plant 98Bd3, of the Hybrid 128 × Rosen second back cross, to all appearances was identical with Hybrid 128, except for kernel color and slight differences in kernel shape. The selfed seed of this plant, in 1928, produced 32 red-kerneled and 82 white-kerneled plants, or a ratio of 1 red to 2.56 white. White kernel color in wheat is recessive, so that the segregation is not the same as that usually obtained in crosses between wheat varieties. The white-kerneled plants were identical in morphological characters with those of the parent, Hybrid 128, except for such variations as are normally found within the variety itself. The kernels of the red-kerneled plants were slightly longer on the average and more or less angular, instead of plump as in the white-kerneled plants and in Hybrid 128. Red-kerneled plants were also less fertile.

The mean fertility of the red-kerneled plants, expressed as the average number of kernels per spikelet, was 1.03 ± 0.047; of the white-kerneled plants, 1.37 ± 0.022; and of the parent plants, 1.77 ± 0.040. All hybrid and parent plants were bagged. The difference in fertility between the red-kerneled and white-kerneled plants was 0.30 in favor of the white-kerneled plants. This difference is 5.8 times its probable error. The factor, or determining element, for the red color apparently caused a reduction in fertility. A significant difference in fertility also was noted between the white-kerneled and parent plants, but this may have been due partly to differences in time of bagging or perhaps to soil variation.

In 1929, when all plants were grown without being bagged, the mean fertility of the white-kerneled plants was 2.05 ± 0.010 and of the parent plants 2.14 ± 0.025 kernels per spikelet. The difference of the means of the two classes of plants was 3.3 times the probable error. The mean fertility of the red-kerneled plants was but 1.90 ± 0.030, which is significantly less than that of the white-kerneled plants.

The increased length of kernel of the red-kerneled plants was not statistically significant in 1928, but there was a significant increase, amounting to four times the probable error, in 1929, when a larger number of plants was examined. There was no significant difference in kernel length between the white-kerneled plants and those of the parent variety in 1928, but in 1929 there was a difference of four times the probable error. In both years the fertility of the parent was significantly higher than that of the white-kerneled segregates.

The progeny of the white-kerneled sib plant 98Bd4 segregated for hairy neck and kernel length in 1928. The decrease in fertility and the increase in length of kernel of the hairy-necked plants, as compared with those of the nonhairy-necked plants, were positive and significant. The nonhairy-necked plants here were significantly lower in fertility than the wheat-parent plants. (Compare with Hybrid 128 parent.)

In family 98B4–2 all plants were hairy necked, but there was segregation for development of hairy neck, for kernel length, and for kernel color. A significantly greater length of kernel and a higher degree of sterility were found in plants classed as heavy and medium-heavy hairy neck than were found in plants having light hairy neck.

The light hairy-necked condition showed slight but not significant decrease in fertility when compared with the nonhairy-necked plants in redkerneled family 98B4–2. There was no significant difference in average length of kernel between the two groups.

The white-kerneled WR_1W_3 family 42A1–23, segregating for hairy neck and kernel length, shows relationships similar to those of 98Bd4 for these two characters. Hairy necked and nonhairy necked plants occurred in a proportion similar to that found in the red-kerneled family 98B4–2.

The segregation in Hybrid 128 × Rosen second back-cross family 98Bd4, true breeding for white kernel, was 16 hairy neck to 44 glabrous (Table 9); the segregation in first back-cross second-generation family 42A1, segregating for color of kernel and hairy neck, was 3 hairy to 4 glabrous. (Table 8.) A hairy-necked selection, 42A1–1, produced 25 hairy neck to 33 glabrous. (Table 9.) The segregation in Kanred × Dakold back-cross family 99Ac7 was 12 hairy neck to 36 glabrous.

In 1928, Kanred × Dakold $WR_1W_1W_2$ family 99Ac7, segregated for hairy-neck but otherwise was true breeding and wheatlike. The fertility of the hairy-necked plants averaged 1.28 ± 0.091 kernels per spikelet compared with 1.47 ± 0.043 kernels per spikelet for the nonhairy-necked plants. (Table 11.) The difference probably is significant, but does not appear to be so on account of the large probable error of the hairy-necked group, due to the high degree of sterility in many plants. Kernel length in the hairy-necked plants is significantly greater than in the nonhairy-necked group.

In 1929, a light hairy-necked selection of the same back cross, 99Ac7–18, produced but one hairy-necked plant in a family of 36. Mean fertility, length of kernel, and other characters of the nonhairy-necked plants were almost identical with those of the Kanred-parent family.

TABLE 11.—*Mean fertility and kernel length in segregating and true-breeding or nearly true-breeding families of wheat×rye back crosses, 1928 and 1929*

Cross, generation, segregate, and parent	Family	Segregating characters	Year grown	Total plants	Sterile plants	Plants with hairy neck of indicated degree—			Plants with kernels of indicated color		Mean fertility (average of kernels per spikelet)			Mean kernel length		
						Heavy and medium	Light	None	Red	White	Mean	Probable error	Diff.$_m$ / P. E.$_m$	Mean	Probable error	Diff.$_m$ / P. E.$_m$
Hybrid 128×Rosen:	*No.*			*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*			*Mm.*		
$WR_1W_1W_2$	[b] 98Bd3	Kernel color	1928	114				114	32	82						
Red kerneled				32							1.07	±0.047	5.8	5.7	±0.038	2.4
White kerneled				82							1.37	±.022		5.6	±.019	
													8.8			1.7
Hybrid 128 [b]				10							1.77	±.040	8.4	5.5	±.056	6.3
Hybrid 128 [c]				20							2.26	±.042		5.7	±.023	
$WR_1W_1W_3$	[b] [d] 98Bd3	Kernel color	1929	264				264	90	174						
Red kerneled				90							1.90	±.030	4.7	5.9	±.022	4.0
White kerneled				174							2.05	±.010		5.8	±.012	
													3.3			4.3
Hybrid 128 [c]				41				41		41	2.14	±.025		5.9	±.020	
$WR_1W_1W_2$	[b] 98Bd4	Hairy neck and kernel length.	1928	60	2	5	11	42		58						
Hairy neck				16							.57	±.049	7.2	6.2	±.071	4.5
Nonhairy neck				43							1.05	±.045		5.8	±.052	
$WR_1W_1W_3$	[c] 98B4-2	Kernel color and kernel length.	1929	30	1	23	6		4	25						
Light hairy neck				6					[e] 1	5	2.05	±.111	5.6	6.8	±.041	1.3
Heavy and medium-heavy hairy neck.				[f] 23					3	20	1.27	±.085		6.9	±.067	
WR_1W_2	[c] 42A1-37	Hairy neck and kernel length.	1929	52	21	2	20	30	39	1						
Light hairy neck				11	9						.56	±.116	.7	6.6	±.121	.6
Nonhairy neck				19	10						.77	±.111		6.5	±.098	
WR_1W_3	[c] 42A1-23	Hairy neck and kernel length.	1929	37		5	5	27		37						
Hairy neck				10							1.70	±.086	3.6	6.6	±.089	5.1
Nonhairy neck				27							2.04	±.040		6.1	±.042	
Kanred×Dakold:																
$WR_1W_1W_2$	[b] 99Ac7	Hairy neck	1928	48		5	7	36	48							
Hairy neck				12							1.28	±.091	1.9	7.1	±.096	4.7
Nonhairy neck				36							1.47	±.043		6.6	±.046	

$WR_1W_1W_2$	[a] 99Ac7–18	Hairy neck	1929	36			1	35	36		2.00	±.030		6.7	±.037		
$WR_1W_1W_2$	[a] 99Ac1	Kernel length	1928	67				67	67		2.06	±.020		6.8	±.021		
$WR_1W_1W_2$	[a] 99Ac8	True breeding or nearly so.	1928	56				56	56		2.01	±.025		6.7	±.038		
$WR_1W_1W_3$	[c] 99Ac8–23	do	1929	[g] 43				43	43		1.77	±.035		6.8	±.030		
$WR_1W_1W_3$	99Ac8–35	do	1929	35				35	35		1.89	±.014		6.8	±.019		
Kanred × Rosen:																	
$WR_1W_1W_2$	[c] 400Aa1	do	1928	64				64	64		1.98	±.019		6.5	±.024		
$WR_1W_1W_2$	[c] 400Aa6	do	1928	62				62	62		1.82	±.033		6.5	±.027		
$WR_1W_1W_2$	400Cc1	do	1928	[h] 54				54	54		1.66	±.043		6.8	±.032		
$WR_1W_1W_3$	[c] 400Cc1–3	do	1929	[f] 34				34	34		1.83	±.033		7.0	±.036		
$WR_1W_1W_3$	[c] 400Cc1–7	do	1929	[i] 33				33	33		1.88	±.027		7.2	±.028		
Kanred			[b] 1928	10				10	10		1.72	±.034	3.5	6.3	±.048	6.1	
Do			[c] 1928	25				25	25		1.93	±.050		6.6	±.012		
Do			[c] 1929	44				44	44		2.02	±.020		6.8	±.020		

[a] Probable error of difference of probable errors $\sqrt{(P.E._1)^2+(P.E._2)^2}$.
[b] Plants bagged to prevent contamination by foreign pollen.
[c] Plants not bagged.
[d] Progeny of 10 red-kerneled plants from F_2 family 98Bd3.
[e] Dull red.
[f] Including one semidwarf.
[g] Two grassy dwarfs additional.
[h] One grassy dwarf additional.
[i] Plus two dwarfs.

Wheatlike Families of Parent Type

In 1928, Kanred×Dakold $WR_1W_1W_2$ family 99Ac8, having 56 plants, apparently was again completely fertile, since it was higher in fertility than the Kanred parent. However, length of spike and length of kernel were slightly greater than in the Kanred parent. (Table 11.)

In 1929, two selections from the same family, 99Ac8–23 and 99Ac8–35, produced families both of which were slightly lower in fertility than the Kanred parent. Family 99Ac8–23 had four grassy dwarfs, which normally are not found in Kanred. Dwarfs may indicate some sort of chromosome irregularity.

In 1928, Kanred×Rosen $WR_1W_1W_2$ families 400Aa1 and 400Aa6 were true breeding and of Kanred type. Height of plant, length of spike and kernel, fertility, and other plant characters were normal. (Table 11.) These selections evidently had returned to the parent type.

DISCUSSION

The varieties of common wheat used in this experiment cross quite readily with Rosen and Dakold ryes. The F_1 was completely sterile when the plants were protected from contamination by foreign pollen. Unprotected plants yielded up to about 0. 6 per cent of viable kernels. These results agree with those of Jesenko (*8*), Meister (*12*), Leighty and Taylor (*11*) and others. Such results are not unexpected in view of the extent of chromosome incompatibility found in wheat ($n^7=21$)×rye ($n=7$) hybrids. The small set of fertile seed obtained from back crossing or from open pollination shows, however, that a small proportion of viable ovules are formed. It seems likely that both male and female gametes of similar constitution may be produced. The chances of two gametes capable of fertilization coming together would be so remote that self-sterility is complete for all practical purposes. Watkins (*17*) concluded from a study of hybrids of a cross of *vulgare*×*turgidum* wheats that sterility is due in most cases to lack of functional pollen. The situation in wheat×rye hybrids is not strictly comparable but is probably similar; therefore, with relatively high mortality in the pollen cells, the chance of obtaining selfed seed in F_1 wheat×rye plants is extremely small. No such seed has been obtained. When normal pollen is used a small degree of fertility is displayed.

When the back crosses of the several wheat×rye hybrids were grown the plants from each parent pair were more wheatlike than those from the F_1 parent, but there was variation among them. Certain plants exhibited more rye characters than others, while an occasional plant was very similar to the wheat parent. Such results might be expected from random distribution of the chromosomes. Kihara (*9*) and Thompson (*16*) report that random distribution of the chromosomes occurs in F_1 wheat×rye hybrids. However, there is in operation another type of chromosome distribution, which results from the formation of somatic gametes. This is discussed more fully by the author in a paper on a cytological study of this same wheat×rye×wheat hybrid material (*5*). The different types of plants obtained showed distinct variability in the chromosome constitution of the ovules of the F_1 wheat×rye.

[7] n=any number of chromosomes.

The degree of sterility was reduced by back crossing, but variability of plant characters was increased. Nineteen viable WR_1W_1 kernels produced 14 completely sterile plants; 51 viable $WR_1W_1W_1$ kernels produced only 8 completely sterile plants. The repeatedly back-crossed plants became more wheatlike with increased fertility, presumably a direct result of the elimination of rye chromosomes. A similar return to more wheatlike forms was noted in back-crossed material that was selfed.

Several lines were obtained from the second back cross that apparently closely conformed to the wheat-parent type. They were wheatlike and fully fertile.

The white-kerneled plants segregating from the red-kerneled wheatlike strain 98Bd3, of the Hybrid 128 × Rosen back cross, appeared to be identical with Hybrid 128 both in plant characters and fertility. The red-kerneled plants were somewhat reduced in fertility. The kernels of the latter were angular and on the average slightly longer than those of Hybrid 128. Length of spike also was slightly increased. The factor for hairy neck similarly reduced fertility and slightly modified the expression of plant characters. Apparently the presence of rye factors or of elements carrying such factors sets up a state of unbalance which interferes with the normal functioning of the wheat-chromosome system.

It has been mentioned that the red-kerneled $WR_1W_1W_1$ Hybrid 128-like plant, 98Bd3, was the ancestor of a strain wheatlike in all characters but kernel color. The $WR_1W_1W_2$ family grown in 1928 produced a ratio of one red kernel to 2.56 white kernels. Red-kerneled plants from this progeny produced similar results in 1929. The white-kerneled or recessive plants were always in preponderance. In explaining this apparent reversal of dominance, chromosome constitution must be considered. In one $WR_1W_1W_3$ family the white-kerneled plants were found to have 42 chromosomes, and the red-kerneled 43 and 44 (*5*). The type of segregation obtained evidently resulted from the various recombinations of 21 and 22 chromosome gametes, the red color being carried by the extra chromosome. Similar types of segregation occurred in most hairy-necked and long-kerneled progenies. It is likely that the rye factors producing these characters were added as whole chromosomes.

The occurrence of a nearly true-breeding red-kerneled line and of an apparently homozygous hairy-necked line (in $WR_1W_1W_3$) gives some indication of the possibility of producing wheat-rye strains constant for specific rye characters. It is possible that rye elements may be brought into the wheat-chromosome system by (1) the introduction of rye genes by crossing over, (2) the substitution of a rye pair of chromosomes for a wheat pair, or (3) the addition of rye chromosomes to the normal wheat complement. The limited and loose pairing noted in wheat × rye hybrids does not appear favorable to the transfer of rye genes to wheat by crossing over even if it should be definitely established that the pairing involved a wheat and a rye chromosome. Chromosome substitution has not been demonstrated. The addition of a single chromosome pair may be possible, since pairing and fairly normal reproductive cell divisions were noted in 44-chromosome plants of the red-kerneled progeny of 98Bd3–16.

SUMMARY

Crosses were made between three 42-chromosome and four 28-chromosome wheats and Rosen and Dakold rye. The 42-chromosome varieties were fertilized quite easily with rye pollen, while the 28-chromosome varieties were fertilized with difficulty or not at all.

The F_1 wheat×rye hybrids were completely self-sterile. Both dominant and intermediate wheat or rye characters were present, but in general the F_1 plants were more wheatlike than ryelike.

The F_1 plants produced a small percentage of viable kernels upon back crossing. The F_1 hybrids of Hybrid 128 and Kanred wheats crossed with Dakold and Rosen ryes were back crossed to their respective wheat parents. These back crosses were again back crossed to the same wheat parents. Genetic and cytologic studies were made of the back crosses of Hybrid 128×Rosen; genetic studies only were made of the back crosses of Kanred×Dakold and Kanred×Rosen.

Selfed as well as back-crossed plants in the first back-cross first generation (WR_1W_1) and in the second back-cross first generation ($WR_1W_1W_1$) and second generation ($WR_1W_1W_2$) were covered with manila-paper bags to prevent contamination with foreign pollen. Bagging tends to reduce the normal fertility. In a comparison between bagged and unbagged plants, in 1928, bagging reduced fertility 17.9 per cent in Hybrid 128 and 19.7 per cent in Kanred.

Fertility was increased by back crossing with the parent wheat, and progeny plants became more wheatlike. Viable seeds from the back cross on F_1 produced approximately 74 per cent of sterile plants. Viable seeds from the back crosses on first-generation back-crossed plants (WR_1W_1) produced about 16 per cent of sterile plants. The progeny of selfed plants also tended to become more wheatlike. Parent types were recovered in the second back-cross second and third generations.

Plants that had red kernel color, hairy neck, and long kernel from wheatlike families of Hybrid 128×Rosen back crosses usually exhibited reduced fertility. Those with red kernels appeared least fertile. Plants having light hairy neck were more fertile than those having heavy hairy neck. A wheatlike, nearly homozygous, red-kerneled progeny and an apparently homozygous hairy-necked progeny were obtained, indicating the possibility of producing constant wheat×rye strains.

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A CYTOLOGIC STUDY OF WHEAT×RYE HYBRIDS AND BACK CROSSES[1]

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INTRODUCTION

In a genetic study of wheat×rye hybrids and back crosses reported by the writer (*4*),[3] varieties of the 21-chromosome wheats were crossed with varieties of rye (n=7).[4] Complete sterility was noted in F_1 hybrids. A low percentage of fertility was obtained on back crossing with the wheat parent. The plants thus obtained were more wheatlike than those of the F_1 hybrid, but they showed variation. The WR_1W_1[5] plants obtained in the first back cross were again back crossed with the same parent. From the second back cross, $WR_1W_1W_2$ generation, a wheatlike line was obtained which segregated in a ratio of 1 red-kerneled to 2.56 white-kerneled plants. In similar strains from both WR_1W_3 and $WR_1W_1W_3$ generations, kernel color and "hairy neck" appeared more or less constant. It is evident that a knowledge of the chromosome relationships of the hybrid progeny is necessary to explain the phenomena observed.

REVIEW OF LITERATURE

The cytology of wheat×rye hybrids was first studied in 1920 by Kihara (*7*). He found the somatic chromosome number to be 28. From 1 to 3 bivalents in loose combination and from 28 to 22 univalents were noted in the metaphase. About 26 per cent of the cells counted contained only univalents. Chance distribution of univalents followed by abnormalities in later stages of division was the rule.

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[3] Reference is made by number (italic) to Literature Cited, p. 362.

[4] n=any number of chromosomes.

[5] The designation WR_1W_1 used throughout this paper denotes that the F_1 of the wheat×rye cross (written as WR_1) has been back crossed with the wheat parent, W, resulting in the plant or series of plants in question. The formula without the subscript or generation numeral, as WR_1W, refers to the crossed kernels, or P_1, of the back cross in question. The generation of the back cross is designated by the usual subscript numeral, as WR_1W_1, WR_1W_2, etc. WR_1W_2 indicates that the plant WR_1W_1 has been selfed producing a second generation. Likewise, $WR_1W_1W_1$ indicates that the original F_1 hybrid has been back crossed with wheat and the resulting hybrid again back crossed with the wheat parent, producing the plant thus designated. When this plant is selfed the resulting plant is indicated by $WR_1W_1W_2$, and later selfed generations by the usual subscript numerals 3, 4, etc. In crosses involving unequal chromosomes, or chromosomes that do not pair, plants from the back cross on F_1 usually vary somewhat in type, unlike the F_1 plants of ordinary crosses, owing to variability in constitution of the gametes of the hybrid.

Zalensky and Doroschenko (*18*) found that the chromatin thread uncoiling after synapsis seldom appears double, which they believed indicated lack of conjugation. General phenomena were similar to those observed by Kihara.

Melburn (*10*), in a comparative study of the thin thread or spireme stage in the early meiotic prophases in the parents and in the F_1 wheat×rye hybrid, found identical phenomena up to the first contraction or synizesis stage; i. e., the spireme, which is believed to be composed of univalent chromosomes joined end to end, appears as a double thread in both. This appearance can have no significance in relation to chromosome pairing because it is largely absent in the hybrid. Pairing in the parents begins by the formation of loops (made up of pairs of chromosomes still comparatively long and thin), whose sides approach and anastomose and twist. There is some loop formation in the hybrid, but the loops do not anastomose or twist.

Thompson (*15*) found the same number of bivalent and univalent chromosomes as did Kihara, with similar phenomena in later stages. He believed that the pairing he observed was due to autosyndesis or self-pairing of wheat chromosomes.

Longley and Sando (*9*) observed no pairing in the cross *Triticum vulgare*×*Secale cereale*, but in the cross *T. vulgare*×*S. montanum* (a species closely related to *S. cereale*) from one to three bivalents were seen. However, even in the latter hybrid, bivalents were observed only rarely, and lack of pairing was the rule.

Plotnikov (*11*) found somatic chromosome numbers of 42 to 49 in F_3 plants from spontaneous wheat×rye hybrids. Sterile F_1 plants were pollinated with wheat. Although the F_1 and F_2 were not examined, the author concluded that F_1 gametes may contain from 21 to 28 chromosomes.

MATERIAL

Most of the material studied comprised the hybrid and back-crossed hybrid progeny of Hybrid 128 wheat (*Triticum compactum* Host.)× Rosen rye (*Secale cereale* L.). The material was grown at Davis, Calif., in 1927 and 1928, and at Berkeley, Calif., in 1929. Back crosses involving Kanred wheat (*T. vulgare* Vill.), Red Winter spelt (*T. spelta* L.), and Dakold rye (*S. cereale*) were also investigated to some extent. Back crosses were made only with the wheat parents.

Hybrid 128 is a fully constant, winter-habit, white-kerneled, short, strong-strawed wheat developed at the Washington Agricultural Experiment Station (*2*).

Rosen rye is a winter variety with strong, faintly purple straw, and a long, broad, fairly dense spike. In the experiments here reported kernel color usually was pale red or yellowish, but gray and green kernels nearly always were present. The peduncle just below the spike is more or less heavily pubescent for a distance of about 2 inches. The term "hairy neck," first used by Leighty and Taylor (*8*), will be used to designate this character.

Somatic and pollen mother-cell chromosomes of the parents and F_1 of Hybrid 128×Rosen were studied. Somatic chromosome numbers were determined in WR_1W_1 back-crossed plants of four crosses listed in Table 2. Somatic and pollen mother-cell chromosomes were examined extensively in Hybrid 128×Rosen, WR_1W_3, and $WR_1W_1W_3$.

It would have been desirable to make a similar study of the plant ancestors of the hybrid lines studied intensively in F_3, but this was not done owing to lack of suitable preserved material.

METHODS

Root tips for chromosome counts were collected from plants of the F_1, WR_1W_1, $WR_1W_1W_1$, and certain families of the WR_1W_3 and $WR_1W_1W_3$ generations. Plants from which root tips were to be collected were grown in pots to permit a root development sufficient to supply a suitable number of root tips. This required from two to three months. The earlier samples were collected from plants about 6 weeks old. After collecting the root tips, the plants were transplanted in the field.

The root tips collected in 1926 and 1927 were fixed in chrom-acetic-urea, washed, run through the various solutions of alcohol and xylol, and embedded in paraffin in the usual way. In the fall and winter of 1928–29 nearly the same schedule was used, except that S. Nawashin's fixative, as modified by Karpetschenko, was used.[6] Better fixation with greater definition of chromosomes was obtained with chrom-acetic-formalin than with chrom-acetic-urea.

In the plants having 42 or more chromosomes, greatest success was obtained from sections cut to a thickness of 14μ. In 12μ sections a disproportionately large number of metaphase cells were cut. Heidenhain's iron haematoxylin was used to stain the sections.

Anthers were gathered from fresh material brought to the laboratory. Aceto-carmine was used to stain the temporary slides for pollen mother cells. Slides containing suitable stages were sealed in by a preparation of equal parts of paraffin and gum mastic. Slides properly prepared were preserved in good condition from three to six months.

Most of the material for the temporary slides was collected and examined between 4.30 and 9 a. m. Moderately high to high temperatures were found unfavorable for good division figures. Such temperatures frequently occur at the time of meiosis in cereals where this work was done. The pollen mother cells then pass their stages rapidly. With high temperatures and a serious depletion of soil moisture, the pollen mother cells disintegrate.

CYTOLOGIC INVESTIGATIONS

In normally fertile and constant strains or races of plants the chromosomes pair in meiosis. The importance of a study of cytologic relations is evident in crosses where sterility is complete in the initial cross and where back crossing ordinarily is the only method of regaining fertile strains in which may be combined the desired species characters. Chromosome pairing, chromosome numbers, distribution in meiosis, and tetrad and pollen formation were studied in parents, hybrids, and back crosses.

Most of the chromosome studies were confined to the F_1, the WR_1W_1 back cross, and the WR_1W_3 and $WR_1W_1W_3$ back crosses of Hybrid 128 × Rosen.

[6] Fixative. Solution A: 65 c. c. water, 10 c. c. glacial acetic acid, 1 gm. chromic acid. Solution B: 10 c. c. 40 per cent commercial formalin, 65 c. c. water. Equal parts of A and B were mixed immediately before using.

CHROMOSOME STUDIES OF PARENTS AND F_1 HYBRIDS

The somatic chromosome numbers were 42 and 14 in the wheat and rye parents and 28 in the F_1 of Hybrid 128×Rosen, as previously found by other investigators. No 16-chromosome rye plants were found. Such forms were reported by Gotoh (*5*) and by Belling (*1*) and Emme (*3*). Gotoh believed that occasionally a certain chromosome of the rye complement divides into two pieces, thus accounting for the extra chromosome. He reached this conclusion after finding the total linear length of all chromosomes of the 14-chromosome and 16-chromosome types to be equal. Other investigators believe that the 16-chromosome forms may originate through nondisjunction in the reduction division.

From 0 to 3 bivalents, with 28 to 22 univalents, were found in pollen mother cells in metaphases. No equatorial plate was observed in any first-metaphase cell. Usually the univalents were scattered over the entire cell. Pairing did not occur in normal fashion as in wheat and rye. Telosynaptic unions appeared to be most common, and elongated chromatin threads frequently could be seen between segregating pairs. (Fig. 1, F and I.) Orientation of the dividing bivalents sometimes was transverse to the poles of the segregating univalents. A count of cells was made to determine variation in the number of bivalents per cell. (Table 1.) Cells with two bivalents were most numerous. About 18 per cent of the cells counted had only univalent chromosomes.

TABLE 1.—*Distribution of bivalent chromosomes in metaphase cells in F_1 of Hybrid 128 wheat×Rosen rye*

Bivalents per cell	Cells	
Number	*Number*	*Per cent*
0	17	18.3
1	25	26.9
2	48	51.6
3	3	3.2
Total	93	100.0

Univalents apparently segregated at random, with frequent laggards, although what appeared to be as many as three groups of six or seven chromosomes sometimes occurred. One cell with a tripolar spindle was seen. A few cells were seen with all but one or two univalents at one pole and the remainder at the other pole.

The homotypic division was more normal, with equatorial plates more or less well developed, but the same sort of irregularity as observed in the first division was also seen. Laggards were numerous.

Tetrad formation was irregular, with micronuclei in most cells, resulting from lagging chromosomes. Microcytes were common. These usually form as a result of several chromosomes lagging together. Abnormal tetrads with as many as seven cells were seen. (Fig. 1, K–M.)

Pollen from apparently mature anthers was difficult to obtain. A few transparent pollen cells were found, varying in size from small to large. In aceto-carmine preparations pollen grains occasionally could be seen with a trace of nuclear material. Very few were seen with apparently normal nuclei.

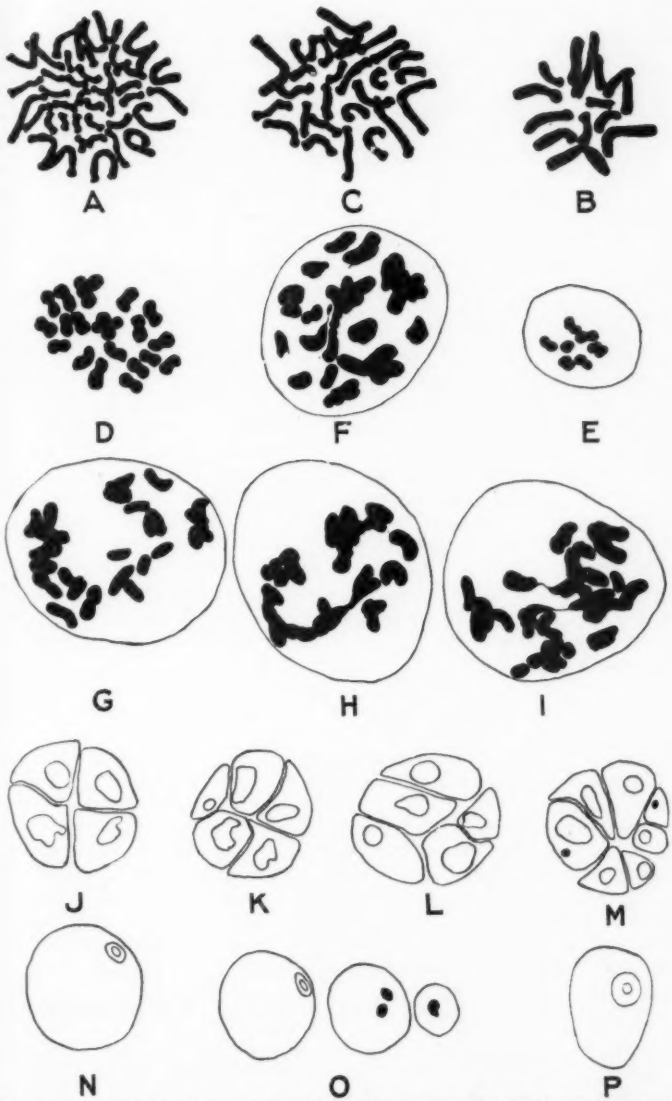

FIGURE 1.—Camera-lucida drawings of somatic and pollen mother-cell division figures from parents and F_1 of Hybrid 128 × Rosen. A.—Somatic-metaphase plate of Hybrid 128 wheat (2n=42). × 2,475. B.—Somatic-metaphase plate of F_1 hybrid (2n=28). × 2,475. C.—Somatic-metaphase plate of Rosen rye (2n=14). × 2,475. D.—Heterotypic-metaphase plate of Hybrid 128 wheat (n=21). × 1,700. E.—Heterotypic-metaphase plate of Rosen rye (n=7). × 1,170. F-I.—Heterotypic-metaphase plate of F_1 hybrid showing cells with all univalents (G), with two bivalents (F and H), and with three bivalents (I). End-to-end pairing best shown in F. × 1,900. J-M.—F_1 tetrads. Most tetrads found were 4 or 5 celled, more or less irregular, usually with one or more micronuclei; microcytes were more or less common; occasional cells were segmented as in L and M. × 1,170. N.—Hybrid 128. Outline of normal pollen grain. O.—F_1 hybrid. Pollen almost absent. Outline of pollen grains showing variation in size. × 1,170. P.—Rosen rye. Outline of normal pollen grain. × 1,170

With the stains used no chromosome differences were observed in either root tip or pollen mother cells that could be used to differentiate the wheat and rye chromosomes in the hybrids. (Fig. 1.)

SOMATIC CHROMOSOME NUMBERS AND PLANT CHARACTERS OF FIRST BACK-CROSS FIRST-GENERATION PLANTS

Somatic chromosome numbers were obtained from root tips of nine artificially back-crossed plants and from the pollen mother-cell count of one plant. Four different back crosses were studied. The chromosome numbers are considered representative of what might be obtained from a random sample from a single hybrid. The chromosome numbers varied from 40 to 49. (Table 2.) The gametic-chromosome numbers of the original F_1 therefore varied from 19 to 28, as only 21-chromosome pollen was used in back crossing. Distribution of plants by chromosome numbers was as follows: One plant each for 40, 41, 43, 44, and 45; two for 47; and three for 49. (Fig. 2, A–G.) It is probable that plants with high chromosome numbers (47 and above) are most common in the first generation after back crossing.

Plants having high chromosome numbers, 47 and above, generally were more wheatlike than those having low chromosome numbers. There was a tendency toward higher fertility in the plants having the highest chromosome numbers. The rye characters when present were reduced in intensity, as in the case of the hairy-neck character in plants 40C3, 44D1, and 44G1. (Table 2.)

The somatic-chromosome number of plant 42C1 was approximately 49. Owing to poor fixation of material it was not possible to get an exact count. This plant was the first-generation ancestor of family 98Bd3–16, a wheatlike family segregating only for kernel color, which was studied cytologically in F_3. A metaphase count could not be obtained, but cells were found which showed in side view as many as five chromosomes outside the equatorial plate. Some evidence of six or seven extra univalents in this plant was found from examination of pollen tetrads. With few exceptions, tetrad formation was regular, the cells being of about equal size, but numerous micronuclei were seen. Numbers of tetrads with micronuclei in high numbers were as follows: One with 12, two with 11, one with 8, two with 6, and one with 5. (Fig. 2, H–K.) The maximum number of micronuclei in a single cell was five, although 4 micronuclei were found in each of two cells in another tetrad. The number of univalent chromosomes making possible such numbers must have been at least six or seven. The observed root-tip count therefore must have been approximately correct.

SOMATIC AND POLLEN MOTHER-CELL STUDIES OF HYBRID 128 × ROSEN FIRST BACK-CROSS THIRD-GENERATION AND SECOND BACK-CROSS THIRD-GENERATION FAMILIES

Chromosome counts on root tips and pollen mother cells in three F_3 families of Hybrid 128 × Rosen back crosses, together with descriptions of their characters as to presence or absence of hairy neck, kernel color, and average length of kernel, are presented in Table 3. Family 98Bd3–16, grown from a red-kerneled selection of family 98Bd3 (fig. 3, C), produced about equal numbers of red-kerneled and white-kerneled plants. Root-tip counts were made on 12 plants in family 98Bd3–16. All white-kerneled plants had 42 chromosomes, and the red-kerneled plants had 43 and 44 chromosomes. Spike characters are shown in Figure 4, B, C, and D.

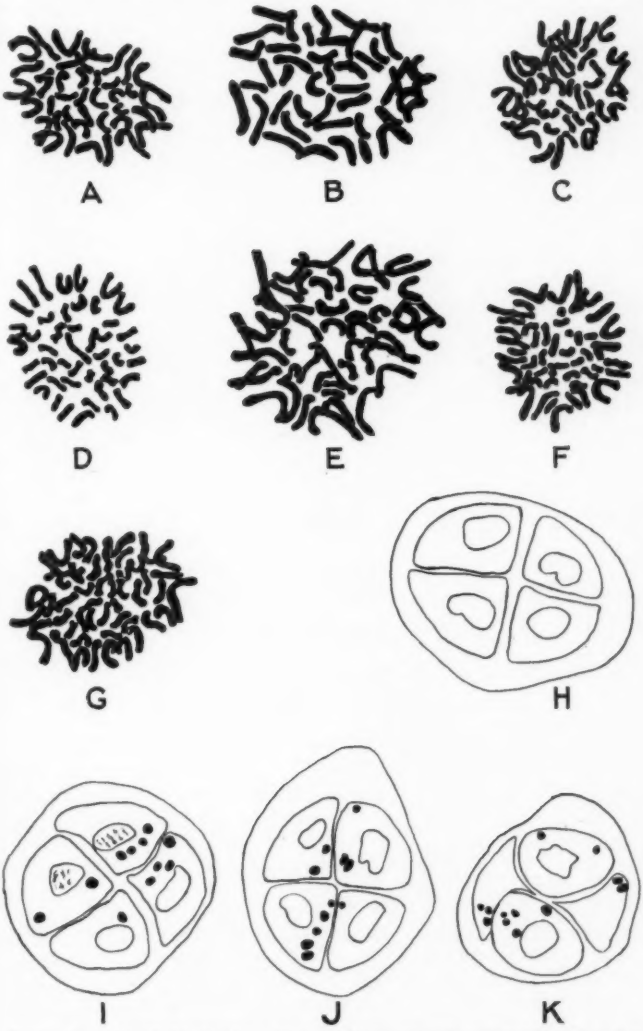

FIGURE 2.—Camera-lucida drawings of somatic chromosomes of seven first back-cross first-generation wheat × rye hybrid plants, and characteristic tetrads of plant 42C1. A.—Somatic metaphase of plant 40E1 (2n=40). × 2,000. B.—Somatic metaphase of plant 42 (2n=43). × 2,600. C.—Somatic metaphase of plant 44E1 (2n=44). × 2,000. D.—Somatic metaphase of plant 42B (2n=45). × 2,600. E.—Somatic metaphase of plant 40C3 (2n=47). × 3,150. F.—Somatic metaphase of plant 44D (2n=49). × 2,000. G.—Somatic metaphase of plant 44F (2n=49). × 2,000. H–K.—Tetrads of plant 42C1, a 49-chromosome plant (approximate number) showing up to 11 micronuclei, resulting from the unpaired rye chromosomes. × 1,225

TABLE 2.—*Character expression and somatic chromosome numbers in first back-cross first-generation wheat × rye hybrid plants*

Back-crossed generation and parent	Back-cross No.	Plant characters				Fertility of selfed plants			Kernel characters			Chromosome number
		Height	Spike length	Head type	Hairy neck	Florets	Kernels	Seed set	Color	Average length	Development	
Red Winter×Rosen:		*Inches*	*Cm.*		*Degree*	*Number*	*Number*	*Per cent*		*Mm.*		*2 n*
SR_1S_1[a]	40E	50	15	Long lax	None	78	1	1.3	Red			40
SR_1S_1[a]	40C3	55	13	do	Light	76	0					47
Hybrid 128×Rosen:												
WR_1W_1	42A1	46	8	Long club	do	88	10	11.4	Red	6.9	Slightly shriveled	43
WR_1W_1	42B1	39	5.5	Dense club	None	84	0	0	do	7		45
WR_1W_1	42C1	49	5.5	do	do	94	2	2.1	do	6	One medium plump; one shriveled	[b] 49
Kanred×Dakold:												
WR_1W_1	43A1		11	Lax	Medium heavy	74	0					[c] 41
Kanred×Rosen:												
WR_1W_1	44D1	36	14.5	do	Light	82	3	3.7	Red	7.3	Badly shriveled	49
WR_1W_1	44E1		6	do	Medium heavy		0					44
WR_1W_1	44F1		11	do	None		0					49
WR_1W_1	44G1	48	13	do	Light at top	98	4	4.1		6.8	Slightly shriveled	47
Hybrid 128[d]			5	Club	None	71	124	1.75	White	5.1	Badly shriveled	42
Kanred[e]			10	Lax	do	283	672	2.37	Red	6.9	Plump	42
Red Winter[f]		40	13	Long lax	do	83	104	1.26	do	8.1	Medium plump	42

[a] S=spelt.
[b] Approximately.
[c] From gametic chromosome number 20-II+1-I.
[d] Average of 2 plants.
[e] Average of 10 plants.
[f] Average of 4 plants.

TABLE 3.—*Character expression and somatic and gametic chromosome numbers in three back-crossed families of Hybrid 128 × Rosen, 1929*

Back-crossed generation, family, and parent plant No.	Progeny plant [a]	Hairy neck (degree)	Kernel color	Kernel length	Chromosome numbers	
					2n	n
				Mm.		
$WR_1W_1W_2$: 98Bd3-16		None	Red	6.0		
	A-1	do	do	6.5	44	22 [b] II
	A-2	do	do	6.7		21 II+1 [c] I
	A-3	do	White	5.7	42	21 II
	A-4	do	do	6.4	42	
	A-5	do	do	6.5	42	
	A-6	do	Red	6.5	43	
	A-7	do	White	6.5	42	
	A-8	do	Red	7.0	43	21 II+1 I
	A-9	do	White	5.9	42	
	A-10	do	do	6.2	42	21 II
	A-11	do	Red	6.4	44	22 II
	A-12	do	White	6.4	42	21 II
	A-13	do	Red	6.4	43	21 II+1 I
WR_1W_2: 42A1-23		Heavy	do	6.6		
	B-1	None	do	6.7	43	21 II+1 I
	B-2	do	do	7.0	44	22 II
	B-3	do	do	6.8	44	
	B-4	Heavy	White	6.8	45	
	B-5	Medium heavy	Red	6.6	45	
	B-6	None	White	6.1	43	
WR_1W_2: 42A1-33		Medium heavy	do	7.4		
	C-1	Heavy	do	8.2	45	21 II+3 I
	C-2	None	do	6.5	42	
	C-3	Medium	do	6.7	45	22 II+1 I
	C-4	Heavy	do	6.4	42	20 II+2 I
	C-6	None	do	6.3	43	21 II+1 I
	C-7	Heavy	do	7.9	47	21 II+5 I
	C-8	Medium	do	7.9	44	
	C-15	None	do	5.8		18 II+4 I
Hybrid 128		do	do	6.5	42	21 II

[a] For convenience capital letters are substituted for the parent-plant number.
[b] Roman numeral II indicates two paired chromosomes, which usually are seen as a double chromosome or bivalent with the members of the pair lying side by side.
[c] Roman numeral I indicates a single unpaired chromosome or univalent.

Pollen mother-cell counts showed 21 bivalents in the white-kerneled plants, and 21 bivalents plus 1 univalent, and 22 bivalents, respectively, in the red-kerneled 43-chromosome and 44-chromosome plants.

Pairing was normal in the 42-chromosome plants, and no laggards were seen in first or second divisions. (Fig. 5, B and C.) Tetrad for mation also was regular without micronuclei, a few being observed in one plant only.

Twenty-one bivalent chromosomes and a single univalent were found in the 43-chromosome plants. (Fig. 5, E.) The univalent was found to lag and to divide in late anaphase, the divided halves going to their respective poles. Second division was normal except for the lagging members of the univalent. Tetrad formation was normal except for the occurrence of micronuclei. No micronuclei were observed in approximately 20 to 40 per cent of the tetrads examined, while from one to two micronuclei per tetrad were found in the remainder. Apparently the extra chromosome was included in the nucleus where no micronuclei occurred.

Normal pairing was found in the 44-chromosome plants. (Fig. 6, B and I.) At metaphase, however, there was a tendency for the members of the extra pair either to precede the main division or to lag. (Fig. 6, C, J, and D.) Most often the early separation took place, as micronuclei were present in only a small number of tetrads.

Somatic chromosomes were counted in root tips of six plants of WR_1W_3 back-cross family 42A1–23, which was segregating for kernel color and hairy neck. In one white-kerneled and in one red-kerneled plant, both without hairy neck, the number was 43. Two red-kerneled, nonhairy necked plants had 44 chromosomes. A red-kerneled plant with medium-heavy hairy neck had 45 chromosomes, and a white-kerneled plant with heavy hairy neck also had 45 chromosomes. In the two 45-chromosome plants the rye characters—heavy hairy neck and long kernels, and medium-heavy hairy neck and red kernels—appear to have been caused by the same number of extra rye chromosomes. (See fig. 7 for spike characters.)

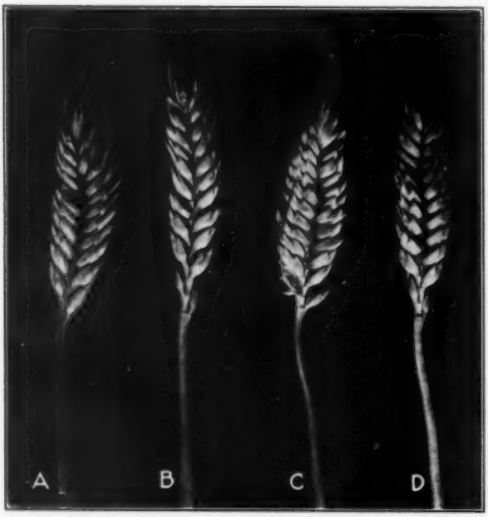

FIGURE 3.—Heads of second back-cross first-generation hybrids and parents. A, WR_1W_1 parent plant, believed to have been originated from somatic gamete. Thus it had an entire somatic complement (2n) of wheat+7 rye chromosomes. When back-crossed to Hybrid 128 (D) it produced plants of type shown in B and C. C was homozygous for wheat with an extra rye chromosome, which is believed to have produced the red kernel color

Pollen mother cells were studied in only two plants of this family. Progeny plant B–1, with red kernels, had 21 bivalents plus 1 univalent, or 20 bivalents plus 3 univalents. From 2 to 3 chromosomes were seen outside the equatorial plate in side view. In homotypic division at late anaphase or early telophase three laggards were seen in both cells of the dividing tetrad. Tetrad formation was fairly normal, with micronuclei in about the same proportion as in the red-kerneled, 43-chromosome plants of family 98Bd3–16. Many micronuclei were in pairs. Ten were single, 20 were double, and 2 were triple. Most pollen grains had micronuclei. It is possible that 3 chromosomes in plant B–1, 1 bivalent and 1 univalent, were rye.

A count of 22 bivalent chromosomes was made in plant B–2. (Fig. 5, J.) In a side view of the equatorial plate and in a number of other metaphase side views one chromosome which looked like a bivalent was seen in three contiguous cells. In second telophase one divided lagging chromosome was seen in each cell of the dividing dyad. Tetrad formation appeared normal, there being micronuclei in only a few cells. This is believed to be a wheat plant with an extra pair of rye chromosomes.

Somatic-chromosome numbers were counted in seven plants of WR_1W_3 back-cross family 42A1–33 segregating for hairy neck and length of kernel. Two plants had 42 chromosomes, two had 45, and the remaining three had 43, 44, and 47. (See fig. 8 for spike characters.)

Both 42-chromosome plants had normal length of kernel (like parent) but one had heavy hairy neck. The latter was believed to have 20 bivalent wheat chromosomes plus 2 univalent rye chromosomes. One of the two 45-chromosome plants, C–1, had heavy hairy neck

FIGURE 4.—Heads of Hybrid 128 wheat parent and of 42, 43, and 44 chromosome segregates of family 98Bd3–16. A, 5 heads from Hybrid 128 parent; B, 7 heads from 42-chromosome plants; C, 4 heads from 43-chromosome plants; D, 2 heads from 44-chromosome plants. The 42-chromosome plants were white kerneled and in all respects identical with Hybrid 128. The 43-chromosome and 44-chromosome plants were red kerneled owing to the presence of an added univalent or a bivalent rye chromosome

and a very long kernel (8.2 mm.). It was found to have 21 bivalents and 3 univalents. The other 45-chromosome plant, C–3, had medium-heavy hairy neck and medium-long kernel. It was found to have 22 bivalents and 1 univalent. Plant C–7, having heavy hairy neck and long kernel (7.9 mm.), had 47 chromosomes, which in meiosis showed 21 bivalents and 5 univalents.

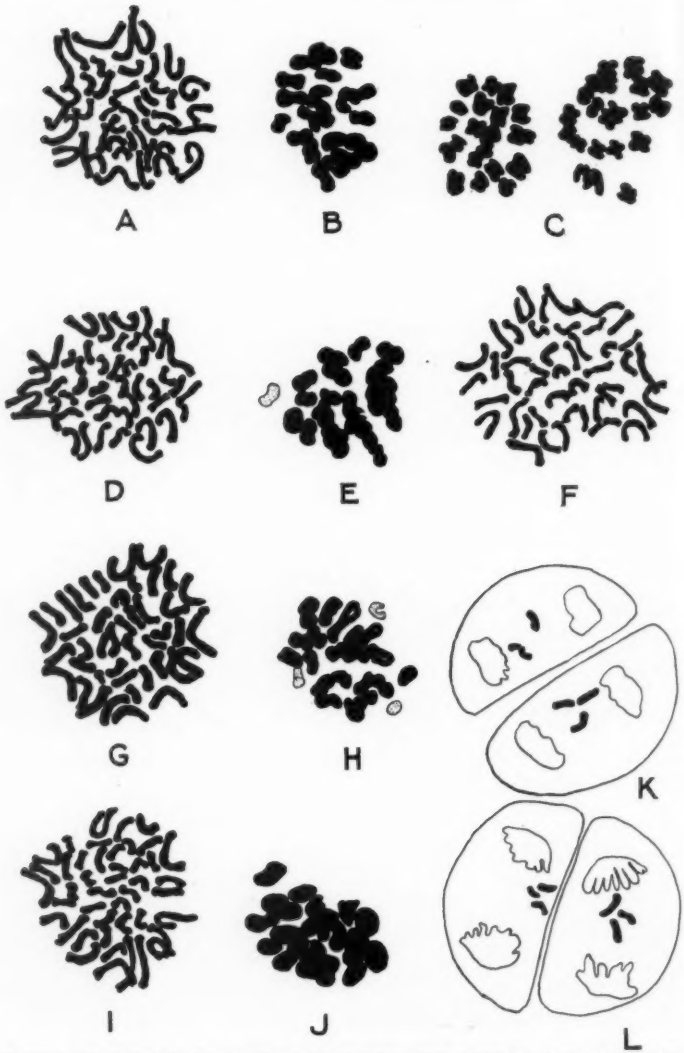

FIGURE 5.—Camera-lucida drawings of somatic and pollen mother-cell division figures of plants from second back-cross third-generation family 98Bd3-16 and from first back-cross third-generation family 42A1-23. A.—Somatic-metaphase plate from plant A-12, white-kerneled plant same as parent type (2n=42). × 2,475. B.—Heterotypic-metaphase plate A-12 (n=21). × 1,900. C.—First anaphase. No lagging, behavior regular. × 1,900. D.—Somatic-metaphase plate from red-kerneled plant A-13 (2n=43). × 2,475. E.—Heterotypic-metaphase plate, A-13 (n=21 II+1 I). × 1,900. F.—Somatic-metaphase plate of B-5, a red-kerneled, hairy-necked plant (2n=45). × 2,475. G.—Somatic-metaphase plate of red-kerneled, nonhairy-necked plant B-1 (2n=43). × 2,475. H.—Heterotypic-metaphase plate of C-1 (n=21 II+3 I). × 1,900. I.—Somatic-metaphase plate of B-2, a nonhairy-necked, white-kerneled, and long-kerneled plant (2n=44). ×2,475. J.—Heterotypic-metaphase plate of plant B-2 (n=22). × 1,900. K-L.—Second telophase of plant B-2 with three lagging chromosomes in each dyad. × 1,900

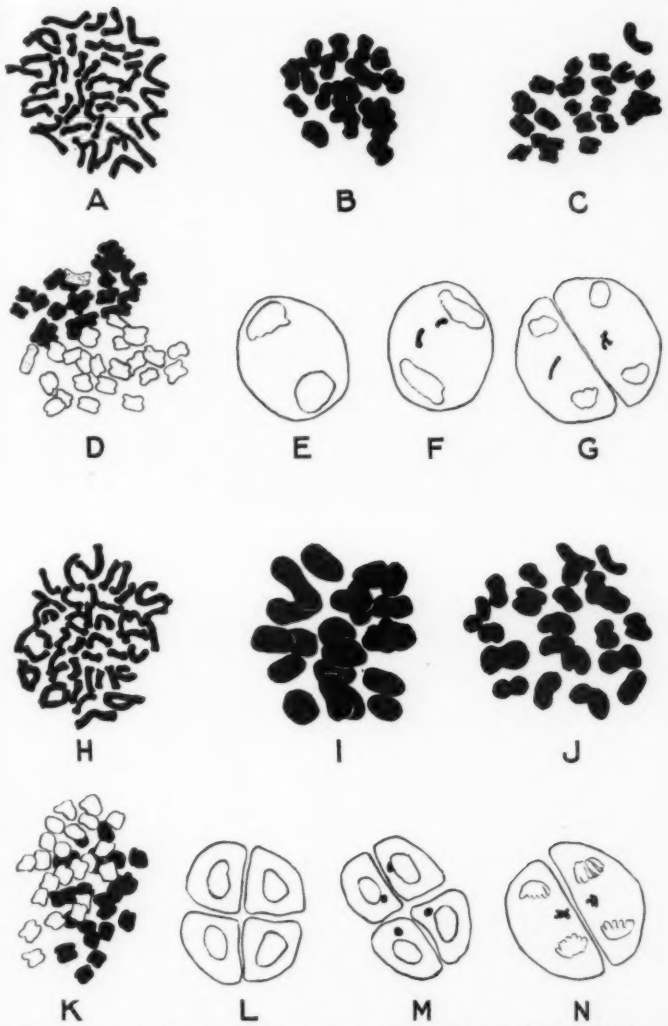

FIGURE 6.—Camera-lucida drawings of division figures from first and second back-cross third-generation hybrid plants of Hybrid 128 × Rosen, including family 98Bd3-16, segregating for kernel color only. A.—Somatic-metaphase plate of red-kerneled plant A-1 (2n=44). × 2,475. B.—Heterotypic-metaphase plate of A-1 (n=22). × 2,475. C.—Heterotypic-metaphase plate of A-1. Both members of extra pair at upper right. × 2,475. D.—First anaphase of A-1; 21 divided chromosomes approaching the poles with the two members of the extra bivalent (stippled) at about the same level between the two groups. × 2,475. E.—First telophase of A-1 showing clean separation. Usually no laggards. × 825. F.—First telophase of A-1 showing members of divided extra pair. Only few cells with laggards. × 825. G.—Second telophase with single and divided chromatid, respectively, in the two cells of the dyad. × 825. H.—Somatic-metaphase plate of red-kerneled plant A-11 (2n=44). × 2,475. I.—Heterotypic-metaphase plate of A-11 (n=22). × 1,900. J.—Heterotypic-metaphase plate of A-11. Divided extra pair at upper right of plate. × 1,900. K.—First anaphase with 22 chromosomes in each group. × 1,900. L–N.—Tetrads of plant A-11. Mostly regular as in L, but laggards also seen in a few cells. M shows one micronucleus in each cell of the tetrad. N shows a dividing chromatid in each cell of the dyad. × 825

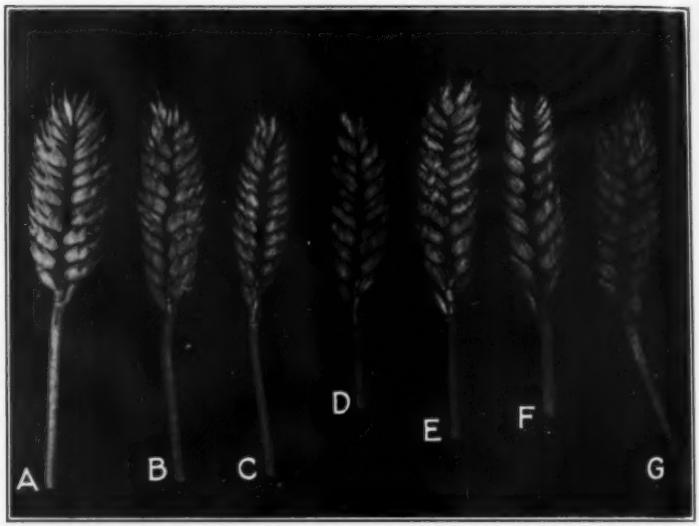

FIGURE 7.—First back-cross second-generation parent spike and third-generation segregates of Hybrid 128 × Rosen family 42A1–23 A, Parent head; B–G, segregates. Chromosome numbers of segregates: B and C, 43; D and E, 44; F and G, 45. E and F were hairy necked; the remainder, glabrous

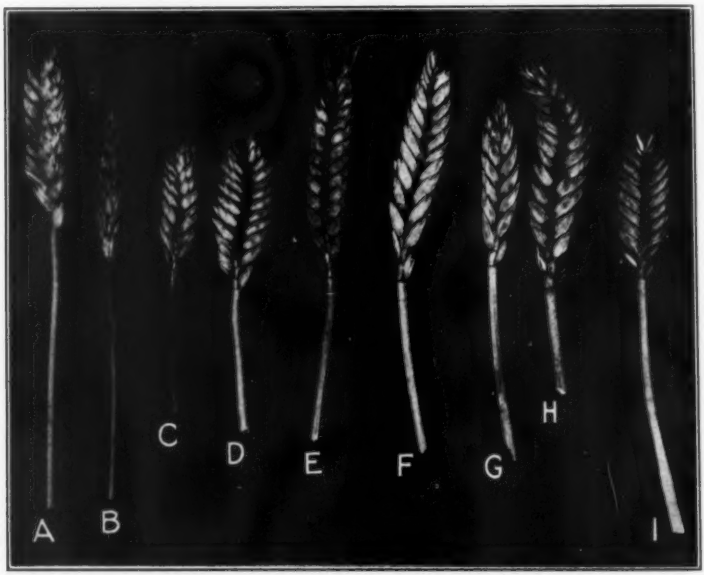

FIGURE 8.—First back-cross second-generation parent spike and third-generation progeny heads of Hybrid 128 × Rosen family 42A1–33. A, Parent head; B–I, WR_1W_3 segregates. Chromosome numbers of segregates: B, 40; C and D, 42; E, 43; F, 44; G and H, 45; I, 47

Examination of pollen mother cells in seven plants of this family showed that pairing was on the whole quite normal, although unpaired chromosomes were found in all plants. Micronuclei were seen in all tetrads. Pollen grains with micronuclei frequently were observed to disintegrate.

Plant C–4, having heavy hairy neck, had 42 chromosomes, 20 of which were bivalents and 2 univalents. (Fig. 9, B.) This plant was a little below normal in stature and had reduced fertility and badly shriveled kernels. Reduction division seemed to proceed normally, however, and no lagging was observed in first anaphase, although there was some lagging in second anaphase.

In plant C–7, with 47 chromosomes, the 21 bivalents with the 5 univalents were easily distinguishable. (Fig. 9, F.) The latter were near the periphery of the metaphase group. They were more slender and usually more curved than the bivalents. A variable number of laggards were seen in the second-division figures (up to two and three) in each cell. Tetrads with micronuclei were the rule. A few tetrads with microcytes were seen. Pollen grains were variable in size. Plant C–7 was more reduced in stature than plant C–4. It had heavy hairy neck and long kernel (7.9 mm.).

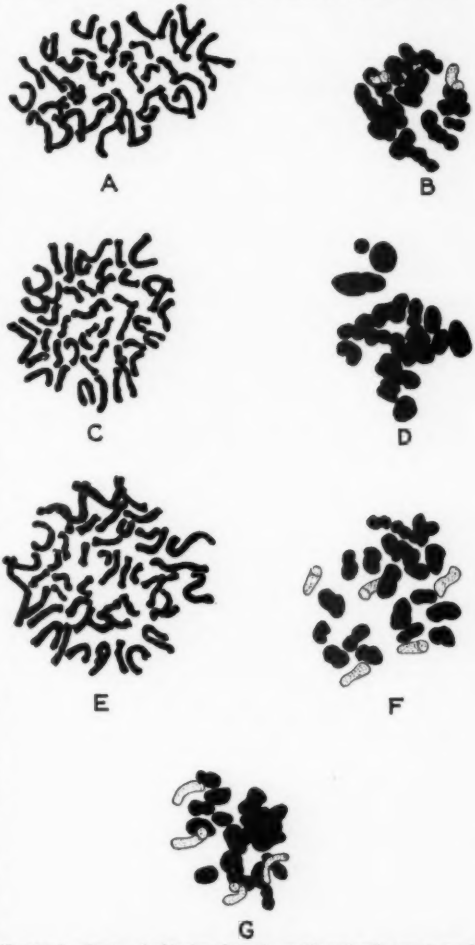

FIGURE 9.—Camera-lucida drawings of somatic and pollen mother-cell division figures of plants from first back-cross third-generation family 42A1-33, segregating for hairy neck and long kernel. A.—Somatic-metaphase plate of heavy hairy-necked, white-kerneled plant C–4 (2n=42). × 3,450. B.—Heterotypic-metaphase plate of C–4 (n=20 II+2 I). Univalents stippled. × 2,640. C.—Somatic-metaphase plate of hairy-necked, white-kerneled plant C–3 (2n=45). × 3,450. D.—Heterotypic-metaphase plate of C–3 (n=22 II+1 I). Univalent stippled. × 2,640. E.—Somatic-metaphase plate of heavy hairy-necked, long-kerneled, and white-kerneled plant C–7 (2n=47). × 3,450. F.—Heterotypic-metaphase plate of C–7 (n=21 II+5 I). Univalents stippled. × 2,640. G.—Heterotypic-metaphase plate of plant C–15 (n=18 II+4 I). Plant reduced in stature, culms slender, neck glabrous, nearly sterile (four kernels from 15 heads). × 2,640

Only a pollen mother-cell count was made on plant C–15. On account of scarcity of material, root-tip counts could not be obtained.

The plant was interesting because it was very much reduced in size. Its culms were slender, with slender spikes, long glumes, and no hairy neck. Sterility was complete except for a few kernels (four in 15 heads), which probably resulted from chance pollination. This plant was found to have 18 bivalents plus 4 univalents. (Fig. 9, G.) Tetrad formation proceeded quite regularly, but micronuclei were present in most cells. No mature pollen was obtained, but droughty conditions may have been partly responsible for its absence.

Micronuclei

The results of a study of the number of micronuclei found in tetrads of first and second back-cross third-generation plants are presented in Table 4. The presence of micronuclei is important, for they indicate lagging and unpaired chromosomes.

Table 4.—*Relationship of the number of micronuclei to the number of gametic chromosomes and to hairy neck and kernel color in first and second back-cross third-generation hybrids of Hybrid 128×Rosen, 1929*

Back-crossed generation, parent, and progeny-plant No.	Tetrads with indicated micronuclei						Total tetrads	Gametic chromosomes	Hairy neck	Kernel color
	None	One in one cell only	One in each of 2 cells	One in each of 3 cells	One in all 4 cells	Variable				
$WR_1W_1W_2$:	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number and kind*		
98Bd3–16—										
A–2	6	14	14				34	21 II +1 I.	None	Red.
A–6	17	16	16				49	[a]43	do	Do.
A–8	9	5	7				21	21 II+1 I.	do	Do.
A–13	18	34	27			1	80	21 II+1 I.	do	Do.
A–1	50	2		4	2		58	22 II.	do	Do.
A–11	13	5	1	3		1	23	22 II.	do	Do.
A–3	89						89	21 II.	do	White.
A–5	51						51	[a]42	do	Do.
A–10	40						40	21 II.	do	Do.
A–12	58		2				60	21 II.	do	Do.
WR_1W_2:										
42A1–23—										
B–1	11	29	22	1	1		68	21 II+1 I.	do	Red.
B–2	22	1	1	1			25	22 II.	do	White.
WR_1W_2:										
42A1–33—										
C–3	8	16	6	1		1	31	22 II+1 I.	Medium heavy	Do.
C–4	17	13	4				34	20 II+2 I.	Heavy	Do.
C–6	36	26	4	2			68	21 II+1 I.	None	Do.
C–7	5	2	3				10	21 II+5 I.	Heavy	Do.
C–15	18	41	33	1			93	18 II+1 I.	None	Do.
Hybrid 128	[b]							21 II.	do	Do.

[a] Somatic-chromosome numbers.

[b] No micronuclei observed.

In family 98Bd3–16, segregating for kernel color only, the white-kerneled plants showed no micronuclei, as division proceeded normally. The red-kerneled, 43-chromosome plants had from one to two micronuclei in one or more cells of most tetrads, owing to the lagging univalent. The 44-chromosome plants with 22 bivalents were without micronuclei in most tetrads. A few tetrads had a single micronucleus in each of the four cells. Some pollen sterility would be expected in such plants.

The conditions as to micronuclei in 22-bivalent-chromosome plant B–2 (family 42A1–23) were similar to those in the 22-bivalent-chromosome plants described in the preceding paragraph. Micronuclei were present in varying numbers in all the remaining plants of family 42A1–23.

Development of Pollen Grains

A study of pollen grains was made on the WR_1W_3 and $WR_1W_1W_3$ plants whose chromosome number had been determined, and on F_1 hybrid plants. Data on chromosome number, presence or absence of hairy neck, kernel color, and length of kernel are shown in Table 5. Counts were made on 7 plants in family 98Bd3–16, on 2 plants in family 42A1–23, and on 5 plants in family 42A1–33.

Apparently normal pollen-grain development occurred in the 42-chromosome white-kerneled plants of family 98Bd3–16. This family, as already stated, was segregating for kernel color only. From 95 to 98 per cent of normally nucleated pollen grains were found. Sixty-five and 56 per cent of normally nucleated pollen grains were found in the red-kerneled plants A–1 and A–11, respectively, each having 22 bivalent chromosomes.

The presence of the rye chromosomes probably was responsible for part of the poor pollen development. Similar results were obtained from the red-kerneled 43-chromosome plants.

The percentages of normal pollen found in families 42A1–23 and 42A1–33 varied from low to medium. On the average the percentage of apparently normal pollen varied with the number of univalents present. Plant B–1, however, with a chromosome number of 43, of which 1 bivalent and 1 univalent are believed to have been rye, produced only 16 per cent of normal pollen. Plant B–2, with 22 bivalent, 1 of which is believed to have been rye, also produced a low percentage of normal pollen, although slightly higher than that of plant B–1.

The presence of rye chromosomes seemed to interfere with normal pollen development, but dry, hot weather at blossoming time also may have been partly responsible for the high degree of sterility, which was found even in some plants of the parent Hybrid 128. About 99 per cent of normal pollen was found in most plants of the parent Hybrid 128, and 69 per cent in the parent Rosen. Only 1 nucleated pollen grain among 413 was found in the F_1 of Hybrid 128 × Rosen.

DISCUSSION

Gamete Formation in F_1

Hybrids between wheat and rye have been shown to be completely self-sterile. When such F_1 hybrids are back crossed to wheat a low percentage of fertility is obtained. The hybrid gametes responsible for this limited fertility appear to originate in two ways: (1) By random distribution of unpaired chromosomes; and (2) by the formation of somatic gametes. The occurrence of the first type is common where univalent chromosomes are found and has been demonstrated by numerous investigators of various plant hybrids. The occurrence of somatic gametes in plants (*Hieracium* sp.) was demonstrated by Rosenberg (*12*). He found that the heterotypic division was interrupted at about late prophase or metaphase and a new nucleus reconstituted with the diploid number of chromosomes.

The chromosome numbers in ovules of the F_1 hybrid were determined by back crossing to the wheat parent. Somatic-chromosome numbers varied from 40 to 49 in 10 progeny plants. The chromosome number of the pollen gamete was 21. Therefore, the chromosome

TABLE 5.—*Pollen grains, gametic chromosomes, hairy neck, kernel color, and kernel length in first and second back-cross third-generation hybrids of Hybrid 128×Rosen, 1929*

Back-crossed generation, parent, and progeny-plant No.	Pollen grains—				Remarks	Gametic chromosomes	Hairy neck	Kernel color	Kernel length
	Nucleated with micronuclei	Empty	With normal nuclei only						
$WR_1W_1W_3$:						*Number and kind*			
98Bd3-16—	*Number*	*Number*	*Number*	*Per cent*					*Mm.*
A-2		80	270	77	Mostly normal	21 II+1 I	None	Red	6.7
A-8	6	108	141	55	do	21 II+1 I	do	do	7.0
A-1		153	279	65	Size uniform, round	22 II	do	do	6.5
A-11		44	56	56	do	22 II	do	do	6.4
A-3		21	634	97	Normal, uniform, some disintegrating	21 II	do	White	5.7
A-10		5	236	98	do	21 II	do	do	6.2
A-12	3	9	230	95	Normal, well developed	21 II	do	do	6.4
WR_1W_3:									
42A1-23—									
B-1	188	14	38	16	Normal size but mostly micronucleated	21 II+1 I	do	Red	6.7
B-2	87	7	59	39	do	22 II	do	White	7.0
WR_1W_3:									
42A1-33—									
C-1	64	13	157	67	Size variable	21 II+3 I	Heavy	do	8.2
C-3	61	28	290	77	Size uniform	22 II+1 I	Medium heavy	do	6.5
C-4	112	41	113	43	Some with micronuclei disintegrating	20 II+2 I	Heavy	do	6.4
C-6	61	4	133	67	Size uniform	21 II+1 I	None	White	6.3
C-7	2	53	45	45	Size variable	21 II+5 I	Heavy	do	7.9
Hybrid 128		3	217	99	Size uniform, round	21 II	None	do	6.5
Rosen		115	261	69	Size uniform, oval	7 II	Heavy	Pale red to gray	
Hybrid 128×Rosen		412	1	2	Size very large to small. Pollen grains transparent, with nucleated portion in occasional cells.	[a]	Medium heavy		

[a] 28 to 22 univalents+0 to 3 bivalents.

numbers in the ovules must have varied from 19 to 28. The parent ovules of three of these plants had a gametic-chromosome number of 28, and two had 26. The chances of obtaining these numbers with random distribution in the F_1 gametes are negligibly small. Assuming random distribution and equal viability of gametes, the chances were calculated by expanding the binomial $(\frac{1}{2}+\frac{1}{2})^n$, where n is the chromosome number of the gamete. Therefore it is seen that the chance of securing 28-chromosome gametes by random distribution is 1 in about 278,000,000, and the chance of securing 26-chromosome gametes is 1 in 718,000. The fact that one-half of the plants examined originated from 28-chromosome and 26-chromosome ovules seems definitely to exclude random assortment as the only mode of gametic-chromosome distribution.

A small number of viable gametes with chromosome numbers varying from 19 to 22, is entirely possible, for from about 0.1 to 2.5 per cent of such gametes should occur, on the basis of random assortment. Twenty-three-chromosome gametes should occur once in about 2,800 times. The chance of securing gametes with lower chromosome numbers is limited by their ability to form viable combinations. If all or nearly all rye chromosomes come together in a single gamete the latter probably will be viable if fertilized with rye pollen.

The lower and upper limits of gametic-chromosome numbers in somatic gametes in F_1 wheat × rye hybrids can only be surmised. Rosenberg (*13*) noted irregularities in chromosome distribution in somatic gametes. Karpetschenko (*6*), in crosses of Raphanus (n = 9) × Brassica (n = 9), found hybrids with triploid, tetraploid, and other polyploid combinations. Plants were found with chromosome numbers varying slightly from exact polyploid numbers as follows: A hypertriploid, 28–29; a hypertetraploid, 37–38; a hypopentaploid, 40–42; a hypohexaploid, 51–53; a hypoenneaploid, 78. The somatic-chromosome number of WR_1W_1 back-crossed plant 42C1 was counted as 51, but scarcity of material made it impossible to determine definitely this number, and the plant is listed as having approximately 49 chromosomes. Wheat-rye somatic gametes with chromosome numbers above 28 are not beyond possibility. It is interesting to note that the gametic-chromosome numbers 24, 26, and 28 were found, but not 25 or 27. This would seem to indicate that in these cases entire pairs of chromosomes had been eliminated in gametic formation. The limited pairing in the F_1 hybrids would effect changes in the calculated proportion of gametic-chromosome numbers. This probably also hinders somatic-gamete formation in that the dividing pairs initiate early cell formation and chromosome segregation.

The occurrence of somatic gametes in wheat × rye hybrids may have possibilities for amphidiploid combination (both chromosome complements doubled) of wheat and rye. Amphidiploids have been produced by several investigators in a variety of plants. An example of such forms in cereals is given by Tschermak and Bleier (*16*) in their Aegilotricum hybrids (n = 28), from Aegilops (n = 14) × *Triticum dicoccoides* (n = 14) and *T. dicoccum* (n = 14).

STERILITY RELATIONS

The slightly fertile wheat × rye hybrids and back crosses, in successive generations of selfing, increase their fertility with the elimination of rye chromosomes and the return of gametes to the parent wheat type. Fertility appears to vary in strains with different rye characters.

High or nearly complete sterility in the selfed first-generation back-cross plants may result from nonviable pollen and egg cells, or from lethal zygotic combinations, or both. That a low percentage of viable ovules is formed is shown where such plants have been back crossed. The chief cause of sterility in the back-crossed plants from somatic gametes is the presence of extra rye chromosomes which in some way interfere with development. As the number of extra rye chromosomes is reduced the fertility of the plant increases, until with a single extra chromosome or pair of chromosomes fairly high fertility is attained.

The chromosome containing the gene or genes for red kernel color appeared to reduce fertility more than did the chromosomes containing the gene or genes for hairy neck. The chromosome causing hairy neck affects the maternal plants, while the chromosome causing red kernel affects endosperm development and thus, directly, fertility. Chromosomes producing long kernel also reduced fertility.

Extent of hairy neck was found to vary in its relation to fertility. Heavy hairy-necked plants generally were highly sterile, while light hairy-necked plants were decidedly less sterile. Hairy-necked plants appeared to be less sterile in Kanred crosses than in Hybrid 128 crosses. Cytological evidence indicates that two chromosomes or two chromosome pairs were present in the heavy hairy-necked plants. The chromosomes controlling both hairy neck and red kernel color caused a lengthening of the kernel. However, there must be other chromosomes that cause lengthening of the kernel, because long kernels were found in plants that had neither red kernels nor hairy neck.

The factors operating to produce sterility may cause striking changes in plant characters. Frequently there is reduction in height of plant, number of culms, and general vigor. Occasional dwarf plants may appear. More or less badly shriveled kernels are a reasonably certain index of abnormal chromosome relations. Sax (*14*) found in crosses between *Triticum durum* (n = 14) and *T. vulgare* (n = 21) that the weight (endosperm development) of P_1 seeds was about one-half of the mean of the parent seeds. In F_2 endosperm (F_1 plant) the development of seeds varied from plump to shriveled. Sax concluded that small wrinkled grains are characteristic of partially sterile hybrids. Watkins (*17*) found that in crosses between 14-chromosome and 28-chromosome wheats germination and development of grain are determined largely by the chromosome constitution of the endosperm. A high percentage of germination occurs if the *vulgare* chromosomes are all diploid or triploid in the endosperm.

CONSTANT FORMS WITH RYE CHARACTERS

From cytologic and genetic evidence it appears possible to add a pair of rye chromosomes to the wheat complement in a more or less constant combination. The best evidence for this is found in the red-kerneled family 98Bd3–16 of Hybrid 128 × Rosen. This family was found to be pure for all wheat characters except kernel color. The red color was found to be due to the presence of either one or two extra chromosomes. Two 44-chromosome plants produced 22 bivalents in the first pollen mother-cell metaphase. The distribution of chromosomes was nearly normal, although there was some irregularity owing to laggards. Tetrad and pollen formation was fairly normal. Judging by general behavior these plants may breed true in succeeding generations.

Supplementary genetic evidence on the production of a red-kerneled strain may be adduced from family 42A1–37, which was red kerneled in 1929 except for one white-kerneled plant (*4*). This family was high in sterility but segregated for hairy neck and long kernels. The presence of the white-kerneled plant may be explained by the occasional elimination from both pollen and egg cells of the extra chromosome bearing the factor for red color. The union of such gametes would produce a white-kerneled plant.

In 1928 several red-kerneled plants were found which had white kernels also. These varied in number from a few to about one-fourth of all kernels of the plant. The appearance of such plants indicated that somatic mutation must have occurred at an early stage of development of the young plant, causing elimination of the chromosome determining red kernel color. As a result, white kernels were produced in a whole section of the spike.

A strain was obtained which was true breeding for hairy neck and still segregating for other rye characters. It is believed that a hairy-necked wheatlike strain can be produced if chromosomes bearing other rye characters are eliminated.

SUMMARY

Chromosome counts from root tips of Hybrid 128 wheat, Rosen rye, and their F_1 hybrids were 42, 14, and 28, respectively. From 0 to 3 bivalents and from 28 to 22 univalents were found in F_1 pollen mother cells. Cells with two bivalents apparently predominated.

Back crossing with the wheat parent showed that a small number of viable gametes are formed. Somatic-chromosome number in 10 first back-cross first-generation (WR_1W_1) plants (9 from root tips) varied from 40 to 49. The gametic-chromosome numbers of the F_1 ovules, therefore, varied from 19 to 28. The gametes with high chromosome numbers (28 and 26) must have been formed as somatic gametes, those with lower numbers (19 to 21 or 22) probably by random assortment.

Back-crossed plants from somatic gametes usually are more wheatlike and fertile than plants from gametes resulting from random assortment.

Somatic-chromosome counts were determined from root tips in 25 first back-cross third-generation (WR_1W_3) and second back-cross third-generation ($WR_1W_1W_3$) plants. Chromosome numbers varied from 42 to 47.

Chromosome counts on plants of a second back-cross third-generation family of Hybrid 128 × Rosen, segregating only for kernel color, were 42, 43, and 44. Red-kerneled plants had 43 and 44 chromosomes, and white-kerneled plants 42 chromosomes. Twenty-two bivalents were found in pollen mother cells of two 44-chromosome plants, whose subsequent behavior was almost normal. In the white-kerneled plants chromosome behavior was normal.

Two hairy-neck families, one segregating for color of kernel and the other for length of kernel, had somatic-chromosome numbers varying from 43 to 45 in the first family and 42 to 47 in the second family. All plants had from 1 to 5 univalents, except one which had 22 bivalents and whose behavior was fairly normal. Tetrad and pollen formation was abnormal in all.

Cytologic and genetic behavior indicates that by back crossing wheat × rye hybrids with wheat it may be possible to produce constant wheatlike strains possessing rye characters. Rye factors apparently may be added to the wheat complement as whole rye chromosomes.

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THE EFFECT OF CALCIUM FLUORIDE AND PHOSPHATE ROCK ON THE CALCIUM RETENTION OF YOUNG GROWING PIGS[1]

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THE WORK OF OTHER INVESTIGATORS

The experiments of Forbes and his associates (*5*)[2] at the Ohio Agricultural Experiment Station defined in a very complete fashion the relative efficiency of several mineral compounds as calcium supplements in swine nutrition. The minerals tested included limestone floats, precipitated bone flour, special steamed bone flour, rock phosphate floats, and precipitated calcium carbonate. As compared with a nonsupplemented ration, the bone and carbonate preparations did not differ greatly in their ability to increase retention of calcium and to induce the development of strong, dense bone. The rock phosphate, however, was distinctly inferior in these respects, for in hardness, density, and breaking strength, no differences were observed between the bones of pigs that received no minerals and those that received the rock phosphate supplement. The average ash content of the humeri of the pigs fed the various mineral supplements, expressed in grams of ash per cubic centimeter of volume, was as follows: Pigs fed calcium carbonate, 0.5148 gm.; steamed bone flour, 0.5125 gm.; precipitated bone flour, 0.4786 gm.; rock phosphate floats, 0.4459 gm.; no mineral supplement, 0.3756 gm.; control, killed at the beginning of the experiment, 0.4645 gm. The rock phosphate value is distinctly lower than the value for any of the other supplements fed. All the minerals used were fed in daily amounts equivalent to 5 gm. of calcium.

Reed and Huffman (*10*, *11*) reported that when raw rock phosphate was fed to dairy cattle to the extent of 1.5 per cent or more of the grain mixture the animals went off feed, remained below normal weight, and their teeth became very soft and in some instances wore down to the gums. The mandibles of these cattle were much thicker and the surfaces were rougher than those of normal cattle. Buckner, Martin, and Peter (*3*, *4*) found phosphate unsatisfactory as a mineral supplement for laying hens. Hens that received rock phosphate ad libitum were affected with diarrhea and their egg production was impaired; the lot that received no minerals laid 60 per cent more eggs than those that received rock phosphate. Further evidence of the low value of rock phosphate as compared to bone meal is furnished by Tolle and Maynard (*17*), who found that white rats fed rock phosphate in quantities equal to 1.8 per cent of the ration gained in weight more slowly than rats fed bone meal. The teeth of the rats that received rock phosphate showed the changes first observed by McCollum, Simmonds, Becker, and Bunting (*7*) as being due to fluorine in the diet. The

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[2] Reference is made by number (italic) to Literature Cited, p. 372.

average ash content of the bones of the rats fed rock phosphate was 10 per cent less than that of the rats fed bone meal. Phosphate rock also lowered the food consumption and checked the growth of rats fed by Sollmann, Schettler, and Wetzel (*15*).

E. B. Forbes was the first to suggest that the fluorine present in rock phosphate is the cause of its deleterious effects. By the method of Reynolds, Ross, and Jacob (*12*), which was devised especially for the analysis of phosphorite minerals, Jacob and Reynolds (*6*) found brown rock phosphate of Tennessee origin to contain from 2.62 per cent flourine in "run-of-mine material" to 4.08 per cent in carefully selected lump rock. A "fertilizer grade" of the same rock contained 3.72 per cent fluorine, while a high-grade washed and ground rock contained 3.89 per cent. The present writers, following the method of Jacob and Reynolds, found 3.83 per cent fluorine in a fertilizer grade of washed raw rock phosphate of Tennessee origin.

The toxicity of flourine to animals has been frequently observed, and even at levels which might be attained in livestock feeding by the use of rock phosphate as a calcium supplement deleterious effects have occasionally been noted. The results of studies carried on at the Illinois station (*9, p. 594*) indicate that for growing pigs the daily requirement of calcium is about 1.95 gm. at 30 pounds in weight, 2.10 gm. at 50 pounds, 2.25 gm. at 100 pounds, 2.40 gm. at 150 pounds, 2.55 gm. at 200 pounds, and 2.70 gm. at 250 pounds. Assuming a utilization of only 50 per cent of the dietary calcium (*5*) it appears that 5 gm. of calcium per day should be sufficient to meet the need of the normal growing pig for this element. The presence of as much as 3.8 per cent of flourine in raw rock phosphate would necessitate the addition of about 0.60 gm. of flourine to the daily ration (equal to 0.02 per cent or more of the daily food intake) to supply the entire requirement of 5 gm. of calcium. For a pig weighing 50 kgm. (110 pounds) it is apparent that the daily flourine intake on this basis would amount to about 0.012 gm. per kilogram of body weight. Toxic effects have occasionally been observed to follow the feeding of sodium fluoride in equivalent fluorine doses; i. e., 0.027 gm. per kilogram of body weight daily.

Brandl and Tappeiner (*2*) report the results of feeding a dog from about 0.04 to 0.08 gm. of sodium fluoride per kilogram of body weight per day. At the higher levels of fluoride feeding diarrhea and nausea occurred. Rats fed by Sollmann, Schettler, and Wetzel (*15*) received daily doses of 0.00015 to 0.15 gm. of sodium fluoride per kilogram of body weight; at levels of 0.015 to 0.020 gm. no evidence of harmful effects was observed. McCollum, Simmonds, Becker, and Bunting (*7*) fed 0.05 per cent of sodium fluoride (0.0226 per cent of fluorine) to rats in an otherwise normal ration, and found abnormal tooth development and slightly stunted growth. Schulz and Lamb (*13*) fed a ration containing 0.0226 per cent fluorine to rats, with no effects noted, though at higher levels the fluorine appeared to have had a deleterious effect on growth and reproduction. Taylor (*16*) found that when a dairy cow was fed about 0.006 gm. of fluorine daily per kilogram of body weight (assuming a body weight of 500 kgm.) as calcium fluosilicate there eventually resulted a serious disturbance of the appetite and general health and an injurious effect on the teeth; the effects in every way duplicating those obtained by Reed and

Huffman from the feeding of rock phosphate to dairy cows. Schwyzer (*14*) fed rabbits 0.03 gm. of sodium fluoride daily for 10 to 20 days and observed that "some of them lost their appetite and became very emaciated."

The experiments of Bethke, Kick, Edgington, and Wilder (*1*) show that fluorine in the form of sodium fluoride when added to the ration of growing swine may lower the food consumption, retard the gains in weight, and modify the composition of bone with respect to its fluorine content. The fluorine content of the bones was uniformly increased as the fluorine in the ration increased. Also the breaking strength of the bones was low for those bones that contained the most fluorine. The results of analyses of the bones for ash and for the calcium, magnesium, and phosphorus content of the ash, however, show no significant differences which may be related to the fluorine intake. The deleterious effects upon food consumption, gains, and strength of bone were observed to follow the feeding of 0.038 gm. of fluorine daily per kilogram of body weight, but not the feeding of 0.021 gm.

PLAN OF THE EXPERIMENT

In the experiment reported in this paper, the effects of rock phosphate at different levels of intake on the calcium metabolism of growing pigs was compared with the effects of synthetic mixtures of tricalcium phosphate and calcium fluoride containing equal amounts of fluorine. Five young Duroc Jersey-Poland China crossbred pigs averaging about 155 pounds in weight at the start were used in the experiment and were confined in metabolism crates for the entire duration of the test. Their basal ration consisted of 79.5 per cent of ground corn, 15 per cent of soy bean-oil meal, 4 per cent of linseed-oil meal, 1 per cent of cod-liver oil, and 0.5 per cent of salt. The ration was mixed fresh every week or 10 days and was kept tightly covered to prevent spoilage and loss of moisture. A sample was taken from each mixing for analysis for calcium. The pigs were given distilled water to drink and a record was kept of the amount consumed. They were weighed every seven days.

There was added to the daily ration of each pig, 5 gm. of calcium in one of the following forms: (1) Pure tricalcium phosphate, (2) tricalcium phosphate and calcium fluoride combined in different proportions for different pigs, and (3) tricalcium phosphate and rock phosphate in different proportions. Each of the five pigs received a different concentration of fluorine in its mineral mixture, i. e., approximately 0.5, 1, 2, 3, and 3.8 per cent, respectively, but in each case the daily calcium addition was the same, i. e., 5 gm. During the periods in which no fluorine was added to the ration, each pig received daily 5 gm. of calcium as pure tricalcium phosphate. In Table 1 are given the kinds and amounts of the daily mineral additions for each pig in each 2-week period.

TABLE 1.—*Daily mineral additions [a] furnishing 5 gm. of calcium added to the basal ration of each pig*

Period Nos.	Pig 6-9			Pig 24-3			Pig 39-30			Pig 32-30			Pig 6-6		
	$Ca_3(PO_4)_2$	CaF_2	F in mineral	$Ca_3(PO_4)_2$	CaF_2	F in mineral	$Ca_3(PO_4)_2$	CaF_2	F in mineral	$Ca_3(PO_4)_2$	CaF_2	F in mineral	$Ca_3(PO_4)_2$	CaF_2	F in mineral
	Gm.	*Gm.*	*P. ct.*	*Gm.*	*Gm.*	*P. ct.*	*Gm.*	*Gm.*	*P. ct.*	*Gm.*	*Gm.*	*P. ct.*	*Gm.*	*Gm.*	*P. ct.*
1 and 2	12.90	.....	0	12.90	.....	0	12.90	.....	0	12.90	.....	0	12.90	.....	0
3 and 4	12.73	0.13	0.47	12.55	0.26	.95	12.21	0.52	1.90	11.87	0.77	2.84	11.60	0.98	3.62
5 and 6	12.90	.....	0	12.90	.....	0	12.90	.....	0	12.90	.....	0	12.90	.....	0
7 and 8	12.73	.13	.50	12.55	.27	1.00	12.21	.55	2.00	11.87	.82	3.00	11.60	1.03	3.83
9 and 10	12.90	.....	0	12.90	.....	0	12.90	.....	0	12.90	.....	0	12.90	.....	0
11 and 12	11.40	[b] 1.69	.50	9.83	[b] 3.47	1.00	6.56	[b] 7.17	2.00	3.07	[b] 11.12	3.00	.....	[b] 14.60	3.83
13 and 14	12.90	.....	0	12.90	.....	0	12.90	.....	0	12.90	.....	0	12.90	.....	0

[a] The quantities of $Ca_3(PO_4)_2$ were calculated on the assumption that the $Ca_3(PO_4)_2$ was 100 per cent pure and would thus contain 38.739 per cent of Ca. It was found later by analysis to contain but 33.607 per cent of Ca and this percentage value was used in determining the calcium intake of the pigs. The calculations for the amounts of CaF_2 fed in periods 3 and 4 are based on a content of 51.325 per cent of Ca and 48.675 per cent of F (100 per cent pure CaF_2). For periods 7 and 8 the basis of calculation is 48.763 per cent Ca and 46.254 per cent F. An analysis of the CaF_2 for Ca showed it to be but 95.018 per cent pure, containing 48.763 per cent Ca and, by calculation, 46.254 per cent of F. These last two values for Ca and F were used for determining the Ca and F intake for all periods in which CaF_2 was fed. The rock phosphate was found to contain 34.233 per cent of Ca and 3.830 per cent of F.

[b] Rock phosphate.

The calcium balances were determined for consecutive 7-day periods. For each pig there was a fore period of two weeks without fluorine at the beginning of the experiment followed by two weeks of fluorine feeding, and then by alternate 2-week periods of no fluorine and fluorine mineral additions.

The metabolism crates in which the pigs were kept during the experiment were cleaned daily, and the feces and urine for a 24-hour period were collected and weighed. The feces were placed at once in a drying oven in a pan with the collections of the preceding days of the period, and the total feces for the period were dried in the oven to constant weight, ground to a fine powder, and kept in air-tight jars at freezing temperature until analyzed.

After the feces and bits of refused feed were removed from the screen, the screen and bottom of each crate were washed thoroughly with approximately 3 liters of boiling distilled water. These washings were added to the day's urine collection, the total filtered through a 100-mesh sieve and thoroughly mixed. A one-tenth aliquot by weight was taken and preserved by adding hydrochloric acid to approximately 0.41 per cent by weight. The combined aliquots were kept in tightly stoppered bottles at freezing temperature until analysis was completed.

Any feed remaining in the feed boxes or spilled in the crates was weighed and considered in calculating the balances.

The percentages of calcium in the feed samples and in the feces were determined by McCrudden's method (*8*), the calcium oxalate precipitate being titrated with standard $KMnO_4$. McCrudden's method was followed in the analysis of urine; in this case the calcium oxalate was ignited and weighed as calcium oxide.

THE FOOD CONSUMPTION AND GAIN OF THE PIGS

During the last two or three weeks of the experiment all of the pigs showed a tendency to eat less. Several times they vomited, but this could not be attributed to the fluorine content of the ration, since it occurred during periods in which fluoride was not present in the ration as well as when it was. Moreover it occurred only in the case of pigs 6–9, 24–3, and 39–30, which received the lower concentrations of fluorine. At no time did the pigs show by behavior or appearance any reaction that could be definitely ascribed to the fluorine.

Pig 32–30, receiving 3 per cent of fluorine in its mineral supplement during the test periods, appeared to be in an unusually healthy condition for the first eight weeks of feeding. The rate of gain was quite uniform and amounted to from 8 to 10 pounds per week. This period of time included two calcium fluoride periods, and throughout no feed was refused. Early in the ninth week this pig began to refuse the ration as offered and was never back to its previous consumption. Later a skin disease developed and very unsightly sores appeared, particularly on the feet and legs. The animal was not able to stand properly because of sore feet. It was killed and an examination made by Dr. Robert Graham, of the Division of Animal Pathology and Hygiene. It was observed that the bones of the pig were exceptionally soft, though nothing unusual was noted about the growth of the teeth. Particularly striking was an extreme fatty degeneration of the liver, which may or may not have been an effect of fluorine. In practically every period after the eighth week there were one or two days in which feed was refused. This pig drank an unusually large quantity of water, amounting to 5 to 6 liters per day as compared to 3 to 4 liters for the other pigs.

The refusal of food by pig 6–6, although not limited to fluorine-containing rations, was probably the result of a disturbance of the appetite brought about by the character of the mineral intake, which contained the highest percentage of fluorine tested. In the case of pig 32–30 also there is no reason evident for the serious failure in appetite or for the general toxic effects noted, aside from the fluorine in the mineral (3 per cent). Some significance might be attached to the effects of long confinement under unnatural conditions, but the other three pigs on the lower fluorine levels did not show any such effect.

TABLE 2.—*Daily gain or loss in body weight of pigs, in kilograms, during each balance period, and average gains for all periods and all animals*

Period Nos. and mineral supplement	Pig 6-9	Pig 24-3	Pig 39-30	Pig 32-30	Pig 6-6	All pigs
1, control	0.75	1.13	0.75	0.91	0.71	0.85
2, control	.68	.36	.78	.58	.32	.54
3, calcium fluoride	.55	.75	.55	.42	.71	.60
4, calcium fluoride	.71	.58	.65	.81	.42	.63
5, control	.49	.58	.65	.58	.49	.56
6, control	.62	.87	.57	.55	.49	.62
7, calcium fluoride	.55	.62	.52	.62	.45	.55
8, calcium flouride	.68	−.03	.69	.65	.13	.43
9, control	.19	.55	.19	−.29	.26	.18
10, control	.84	.68	.29	.65	−.16	.46
11, rock phosphate	−.26	−.26	.00	−.39	−.03	−.19
12, rock phosphate	.26	.52	−.32	.00	.29	.15
13, control	.17	.14	.45	.11	−.19	.14
14, control	.06	.55	−.13	.00	.10	.12
Average for all periods	.45	.50	.40	.37	.28	.41

The rate of gain of all of the pigs is shown by the curves in Figure 1. In Table 2 are recorded the average daily gains in kilograms for each period. The average daily food intakes for the entire experiment are given in Figure 1. Pigs 6–9 and 32–30, though consuming practically the same average amounts of feed daily, gained 0.45 kgm. and 0.37 kgm. daily, respectively. Pig 32–30 received 3 per cent fluorine in its mineral and pig 6–9 received 0.5 per cent. Pigs 24–3 and 39–30 also consumed on an average practically the same amounts of feed. The rate of gain in the case of pig 39–30, receiving 2 per cent fluorine in its mineral, was 0.44 kgm. daily as compared with a gain of 0.50 kgm. for pig 24–3 receiving 1 per cent. On the basis of these two comparisons, where the food intakes are practically the same, the consumption of calcium fluoride and rock phosphate at the higher levels seems to have produced a correspondingly lower rate of gain.

The average rate of gain of pig 6–6 is low compared with that of the other pigs. The food intake of this pig was also less than the intake of the other pigs, which may explain the lower rate of gain aside from any effect of fluorine. However, inspection of the growth curves in

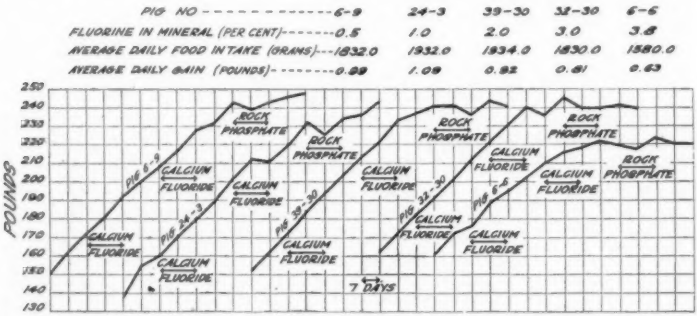

FIGURE 1.—Rate of growth of pigs fed different percentages of fluorine in mineral supplements

Figure 1 shows that there is a progressive decrease in the rate of gain of the individual pigs from pig 24–3, at a 1 per cent fluorine level, to pig 6–6 at a 3.8 per cent level. These results are also indicative of a detrimental effect of fluorine on appetite and on growth, beginning at a level between 1 and 2 per cent of the mineral intake.

Considering Table 2, in which appear the average daily gains in body weight for each pig in each balance period, there are rather extreme differences in the rate of gain shown from one period to another, and such variations may be observed also between periods in which the quality of the ration is exactly the same. It can not be said that any particular variation in weight from one period to another is related to the fluorine intake.

During the first week of the rock phosphate addition, all the pigs either lost in weight or remained stationary. The consumption of food by all of the pigs except pig 24–3 was less during this period, which indoubtedly explains, in part at least, the low rate of gain. None of the pigs returned to their previous level of intake from then on, despite the fact that rock phosphate was not present in the ration of the last two weeks of feeding. These facts suggest a detrimental effect of rock phosphate, even at the lowest level at which it was fed.

There is no evidence that the moisture content of the fecal excretion was affected by the ingestion of calcium fluoride or of rock phosphate, and thus no indication that the calcium fluoride or rock phosphate was either laxative or the reverse.

It seems fair to conclude that, under the conditions of this experiment, the mineral supplements containing 2 or more per cent of fluorine exerted a detrimental effect upon the food consumption and growth of the pigs, and that at levels of 3 per cent or more, distinct deleterious effects resulted. There were indications that rock phosphate exerted a greater detrimental effect than synthetic mixtures of tricalcium phosphate and calcium fluoride containing like percentages of fluorine.

TABLE 3.—*Average daily metabolism of calcium by pigs*

PIG 6-9 (BARROW), 0.5 PER CENT FLUORINE IN MINERAL

Period No.	Intake of fluorine	Calcium intake	Calcium in feces	Calcium in urine	Calcium balance	Calcium retained
	Grams	*Grams*	*Grams*	*Grams*	*Grams*	*Per cent*
1		5.77	3.94	0.06	1.77	30.6
2		5.83	2.92	.05	2.86	49.0
3	[a] 0.0611	5.85	2.80	.05	3.04	51.9
4	[a] .0611	5.88	2.57	.04	3.27	55.6
5		6.08	3.05	.03	3.00	49.3
6		6.08	3.10	.10	2.88	47.3
7	[a] .0643	6.09	3.30	.08	2.71	44.4
8	[a] .0643	5.78	2.43	.04	3.31	57.2
9		5.06	2.62	.04	2.40	47.4
10		5.85	2.85	.03	2.96	50.6
11	[b] .0616	5.20	1.99	.04	3.18	61.1
12	[b] .0651	5.52	3.14	.04	2.35	42.5
13		5.04	2.26	.04	2.73	54.1
14		4.75	2.50	.05	2.20	46.3

PIG 24-3 (SOW), 1 PER CENT FLUORINE IN MINERAL

1		5.80	3.71	0.07	2.20	38.0
2		5.86	3.39	.05	2.42	41.4
3	[a] 0.1217	5.92	3.08	.03	2.80	47.4
4	[a] .1217	5.92	2.94	.04	2.94	49.6
5		6.11	2.85	.06	3.20	52.4
6		6.11	3.45	.04	2.62	42.8
7	[a] .1283	6.13	3.71	.03	2.39	38.9
8	[a] .1283	5.71	2.91	.06	2.73	47.8
9		5.21	3.14	.08	2.00	38.3
10		5.73	2.60	.06	3.07	53.5
11	[b] .1331	5.78	3.38	.06	2.33	40.4
12	[b] .1331	5.41	2.90	.05	2.45	45.3
13		5.54	2.86	.07	2.60	47.0
14		5.59	2.09	.10	3.40	60.7

PIG 39-30 (BARROW), 2 PER CENT FLUORINE IN MINERAL

1		5.89	3.59	0.07	2.22	37.7
2		5.95	3.45	.04	2.45	41.2
3	[a] 0.2422	6.02	3.43	.03	2.55	42.4
4	[a] .2422	6.02	2.82	.05	3.15	52.3
5		6.22	2.87	.05	3.30	53.1
6		6.22	3.26	.03	2.93	47.1
7	[a] .2557	6.25	3.35	.08	2.82	45.1
8	[a] .2557	5.92	3.27	.03	2.61	44.1
9		5.71	3.01	.11	2.58	45.2
10		4.94	1.74	.12	3.07	62.2
11	[b] .2423					
12	[b] .2625	5.40	2.79	.11	2.49	46.1
13		5.34	2.46	.11	2.78	52.0
14		5.04	2.14	.20	2.70	53.6

[a] Fluorine present in the form of calcium fluoride.
[b] Fluorine present in the form of rock phosphate.

TABLE 3.—*Average daily metabolism of calcium by pigs*—Continued

PIG 32-30 (SOW), 3 PER CENT FLUORINE IN MINERAL

Period No.	Intake of fluorine	Calcium intake	Calcium in feces	Calcium in urine	Calcium balance	Calcium retained
1		5.89	4.10	0.04	1.74	29.6
2		5.95	3.44	.06	2.45	41.2
3	[a] 0.3597	6.03	3.21	.01	2.80	46.5
4	[a] .3597	6.03	2.67	.02	3.34	55.4
5		6.22	2.78	.03	3.40	54.7
6		6.22	3.80	.05	2.36	37.9
7	[a] .3808	6.27	3.20	.06	3.01	47.9
8	[a] .3808	5.94	3.64	.06	2.24	37.6
9						
10		5.62	2.25	.03	3.34	59.5
11	[b] .3836	5.41	3.08	.21	2.11	39.1
12	[b] .3421	4.84	2.67	.10	2.06	42.6
13		5.33	3.00	.13	2.20	41.2
14		3.89	2.11	.08	1.70	43.6

PIG 6-6 (SOW), 3.8 PER CENT FLUORINE IN MINERAL

1		5.89	2.27	0.04	3.57	60.6
2						
3	[a] 0.4549	5.87	3.29	.04	2.54	43.2
4	[a] .4185	5.12	2.54	.03	2.55	49.7
5		5.21	2.88	.02	2.31	44.3
6		5.21	2.59	.03	2.59	49.7
7	[a] .4802	6.15	3.37	.03	2.75	44.7
8	[a] .4424	5.38	2.54	.02	2.80	52.1
9		3.98	2.41	.09	1.47	37.1
10		3.89	1.51	.06	2.32	59.7
11	[b] .4566	5.31	2.74	.03	2.55	47.9
12	[b] .5223	5.29	1.86	.04	3.39	63.9
13		4.10	2.13	.04	1.93	47.0
14		4.49	2.14	.05	2.26	50.3

[a] Fluorine present in the form of calcium fluoride.
[b] Fluorine present in the form of rock phosphate.

TABLE 4.—*Daily calcium balances, in grams, of pigs on different mineral supplements with different flourine contents, and of control animals*

[Averages for duplicate successive periods]

Period Nos. and mineral supplement	Pig 6-9, 0.5 per cent fluorine	Pig 24-3, 1 per cent fluorine	Pig 39-30, 2 per cent fluorine	Pig 32-30, 3 per cent fluorine	Pig 6-6, 3.8 per cent fluorine	Average for five pigs
1 and 2, control	2.31	2.31	2.34	2.10	[a] 3.57	2.26
3 and 4, calcium fluoride	3.15	2.87	2.85	3.07	2.54	2.89
5 and 6, control	2.94	2.91	3.12	2.88	2.45	2.86
7 and 8, calcium fluoride	3.01	2.56	2.72	2.62	2.77	2.74
9 and 10, control	2.68	2.53	2.83	[b] 3.34	1.90	2.53
11 and 12, rock phosphate	2.76	2.39	[c] 2.49	2.09	2.97	2.54
13 and 14, control	2.46	3.00	2.74	1.95	2.09	2.45
Average of all periods	2.76	2.65	2.74	2.52	2.45	2.61

[a] Period 1 only. This value is not included in averages because of obvious inconsistency with values obtained for other periods. The cause of this high value is thought to be the incorrect estimation of the amounts of the feces and urine excreted during this period.
[b] Period 10 only.
[c] Period 12 only.

THE CALCIUM BALANCES

The complete balance sheets for the five pigs appear in Table 3. Table 4 is a summary table of the balance data only.

In planning the experiment it was hoped that a response to the fluorine additions might be obtained within a period of two weeks of fluorine feeding. By determining the calcium balance in control periods before and after the fluorine periods, control data were obtained

for comparison with the balances obtained during each period of calcium fluoride and rock phosphate feeding. It was expected that cumulative effect of fluorine would be manifested in the two successive balance periods constituting the after periods.

The data show that the calcium intake was very constant among the different pigs, as well as among the individual periods for each pig. The average daily intake for the entire experiment ranges from 5.070 gm. daily for pig 6–6 to 5.773 gm. for pig 24–3. (Table 3.)

In the distribution of the total calcium excreted no differences exist between the feces and urine that may be related to the fluorine content of the ration. In most periods the average daily calcium in the urine for the period is 0.100 gm. or less, ranging from 0.011 to 0.208 gm., both of which values were obtained for pig 32–30. The average daily amount of calcium excreted in the feces varies from 1.51 gm. for pig 6–6 in period 10, to 4.10 gm. for pig 32–30 in period 1. The average daily calcium content of the feces based on all the periods is 2.820 gm., 3.073 gm., 3.938 gm., 3.075 gm., and 2.484 gm. for pigs 6–9, 24–3, 39–30, 32–30, and 6–6, respectively, receiving successively greater amounts of fluorine in their ration. A slightly lower level of calcium intake in the case of pig 6–6 accounts for the smaller amount of calcium in the feces as compared with that in the feces of the other pigs.

It is more or less obvious after examination of the metabolism data, that there was not an immediate response to fluorine additions or withdrawals in the rations of the pigs. Except in the case of pig 6–6, and possibly of pig 32–30, there is no indication that either calcium fluoride or rock phosphate had any effect on the amount of calcium retained. The daily calcium balances for each pig except 6–6 showed a gradual increase up to the end of the fourth week.

In the case of pigs 6–9, 24–3, and 39–30, no significant variations in the balances of the contrasting experimental periods were evident. However, for pig 6–6 the variations in the balances from week to week may be correlated with the calcium fluoride and rock phosphate additions. The balances for the weeks immediately following the calcium fluoride periods, i. e., periods 5 and 9, as well as that for the week immediately following the rock phosphate period, are considerably lower than the balances of the previous periods. Also in the second week after fluorine feeding there is a return to a higher calcium balance.

The balance data for pig 32–30 do not show any variations from period to period which may be correlated with the fluorine intake, either in the calcium fluoride and rock phosphate periods or in the post periods which follow. However, for the last four periods the calcium balances are consistently lower than for any of the other periods. Pig 32–30 refused to eat properly during these periods and made no gain in weight at this time. It is possible that these are the results of a toxic effect of fluorine.

The calcium balances per kilogram of body weight for each balance period, as well as their period averages, do not reveal any more significant differences between fluorine and nonfluorine periods and between pigs receiving different levels of fluorine in their mineral supplements, than do the absolute balances of calcium and their averages, as given in Tables 3 and 4.

The amount of fluorine in the rations of pigs 32–30 and 6–6 was equivalent to about 0.017 to 0.026 per cent of the daily ration and

represented an intake of about 0.0035 to 0.0055 gm. of fluorine daily per kilogram of body weight. The results of feeding 0.017 to 0.026 per cent of fluorine to these pigs may be regarded as rather definite indication that the calcium retention of growing swine may be affected deleteriously by fluorine. Since fluorine was present in the mineral at 2-week intervals only, a more serious effect would probably have followed a régime of continuous fluorine feeding.

SUMMARY AND CONCLUSIONS

The deleterious effects noted in the literature as the result of the use of raw rock phosphate as a mineral supplement have been attributed by investigators generally to its fluorine content. An attempt has been made, therefore, to study the effect of fluorine, both as calcium fluoride and as it occurs in raw rock phosphate, on the growth, condition, and calcium metabolism of growing pigs.

It was found that mineral supplements containing 2 per cent or more of fluorine appeared to exert a detrimental effect upon the food consumption and growth of pigs, and that fluorine at levels of 3 per cent or more appeared to cause distinct toxic effects. All mineral supplements were fed in amounts furnishing 5 gm. of calcium daily. There were indications that rock phosphate exerted a more detrimental effect than synthetic mixtures of tricalcium phosphate and calcium fluoride containing like percentages of fluorine.

However, the results of feeding fluorides to pigs, even at the highest levels, that is, about 0.017 to 0.026 per cent of fluorine (0.0035 to 0.0055 gm. per kilogram of body weight), can not be regarded as having demonstrated an effect of fluorine on calcium utilization in intermittent periods of feeding, although there were indications, if nothing more, that these high levels of fluorine depressed calcium metabolism.

The experiment as a whole may be taken to indicate that it is inadvisable to supply the entire calcium requirement of pigs by rock phosphate, but that one-third or less of the requirement fed as rock phosphate may not, in a few months time at least, produce deleterious results. However, before the feeding of rock phosphate even at this level can be recommended it must be shown, not only that it is not toxic, but also that it is as efficient a calcium supplement as bone-meal, limestone, and other products of known value.

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EFFECT OF THE STRUCTURE AND MOISTURE OF PLANT CONTAINERS ON THE TEMPERATURE OF THEIR SOIL CONTENTS [1]

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INTRODUCTION

The work presented in this paper is the outgrowth of the observation that the structure of a soil container does influence the soil temperature. The rôle that soil temperature plays in plant growth may not be as apparent as the rôle of air temperature, but any record of air temperature is not a measure of the soil temperature when small containers are used. The experience of this laboratory does not indicate that the choice of a plant container should be influenced by the question of porosity, for as good, if not better, plants have been grown in vitrified containers as in the standard clay pot. Further, the experimental work at this laboratory has not shown that the variable soil temperatures encountered with containers of different structure have any direct effect on plant growth. But soil temperature is of vast importance to the world flora and in particular to the flora of the soil.

PLAN OF THE INVESTIGATION

In order to secure a fairly even air temperature the apparatus used in maintaining constant soil temperatures was adapted to give a constant air temperature. Long, cylindrical, galvanized-iron pots surrounded by water at a high temperature under thermostatic control made it possible to give each pot the same environment. A wire form held the pot in place suspended over the heated air so that it was equally exposed. The common 3-inch clay flower pot was considered as a standard. This pot is known as a medium-burn and is the type most in demand by growers. The ordinary thick glass tumbler holds the same quantity of soil as does the 3-inch pot and was used in these experiments as an example of a pot made of vitreous material. Three other types of commercial pots were employed in these tests: (1) A pot made of compressed peat; (2) a pot of leather fiber and unknown ingredients; and (3) a pot of heavy paper infiltrated with paraffin.

In preparing for an experiment the pots were submerged in water until the pore spaces had become filled. They were well drained before being filled with soil. Water was added to the soil in excess to insure a water contact between the soil and the pot. The pots were left in the same temperature environment overnight. A thermometer in each pot at the same depth made it possible to determine the temperature of the soil at a locus near the middle of the soil mass. The readings were at half-hour intervals over a period of eight hours.

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The publication of all the data obtained would occupy considerable space. Suffice it to state that many experiments were carried through comparing four standard pots with an equal number of each of the other types. The consistent results obtained showed that the tanks heating the air gave an exceptionally high degree of uniformity.

In Table 1 are given the temperatures of the soil in the various pots for two experiments performed under conditions when there was a considerable difference in the greenhouse temperatures. These two experiments are typical of the many experiments and the greenhouse temperatures are not abnormally high, the maixmum being 88° F.[2] in experiment 1, and 101° in experiment 2. The air around each pot was heated by water at 140°, but never reached this point as it was lowered by the air temperature in the greenhouse. The greenhouse air temperatures for the half-hour intervals are also recorded as they indicate certain differences that are apparent in the two experiments, the greenhouse air temperatures ranging from 2° to 15° higher in experiment 2 than in experiment 1.

TABLE 1.—*Temperatures of soil mass in soil containers made of different materials as compared with greenhouse air temperatures*

Time	Temperatures of soil mass in pots of different materials and in the greenhouse in—											
	Experiment 1, Mar. 14, 1929						Experiment 2, Mar. 18, 1929					
	Standard pot	Paper pot	Peat pot	Fiber pot	Glass tumbler	Greenhouse	Standard pot	Paper pot	Peat pot	Fiber pot	Glass tumbler	Greenhouse
	°F.	°F.	°F.	°F.	°F.	°F.	°F.	°F.	°F.	°F.	°F.	°F.
8.30 a. m.	64	67	64	65	68	72	61	64	59	62	70	75
9 a. m.	77	82	73	73	82	84	70	75	66	70	81	90
9.30 a. m.	83	91	79	79	93	85	82	86	77	81	95	97
10 a. m.	85	95	82	84	99	86	86	91	82	86	104	91
10.30 a. m.	85	99	84	86	102	85	86	91	82	88	108	97
11 a. m.	85	100	84	88	104	86	88	95	86	91	113	101
11.30 a. m.	86	100	84	90	105	86	91	99	91	95	116	100
12 m.	86	102	85	90	105	86	91	99	90	95	115	93
12.30 p. m.	85	102	84	90	105	88	90	97	88	93	113	91
1 p. m.	85	102	85	91	105	84	86	94	86	91	110	88
1.30 p. m.	85	102	86	91	105	84	86	93	84	91	110	88
2 p. m.	86	102	86	91	105	84	87	94	85	91	111	95
2.30 p. m.	86	102	86	91	105	85	88	95	86	92	111	93
3 p. m.	86	102	86	91	105	84	88	95	86	92	111	91
3.30 p. m.	86	102	86	91	105	84	86	94	84	91	109	86
4 p. m.	86	102	86	91	105	84	85	93	84	91	109	88
4.30 p. m.	86	103	86	91	105	88	86	95	84	91	109	93

The data of experiment 1 are also presented as a graph in Figure 1. It is quite apparent that the porous pots of clay and peat gave the lowest temperatures. The nonporous pots of glass and paraffin-protected paper gave the highest temperatures. The fiber pot is somewhat resistant to the absorption of water and this fact causes its soil temperature to come between those of the vitreous and porous materials.

Particular evidence that the variations of temperature found in the soils contained in pots of different structure is related to water evaporation was determined by an experiment with the peat pots. When

[2] The temperature readings were secured in degrees centigrade but are recorded in degrees Fahrenheit, as this latter scale is the usual measure of air temperature.

peat pots are soaked in water in a nested arrangement (one pot partly surrounded by another) it is practically impossible to moisten them thoroughly. In Table 2 are presented the temperature data showing the relative uniformity obtained in four standard pots and the considerable variation in peat pots that were approximately one-half, two-thirds, and completely moistened. The dry area of the improperly moistened peat pots was the means of determining the approximate area of the nonevaporating surface, which was reflected in the higher soil temperatures found in these pots.

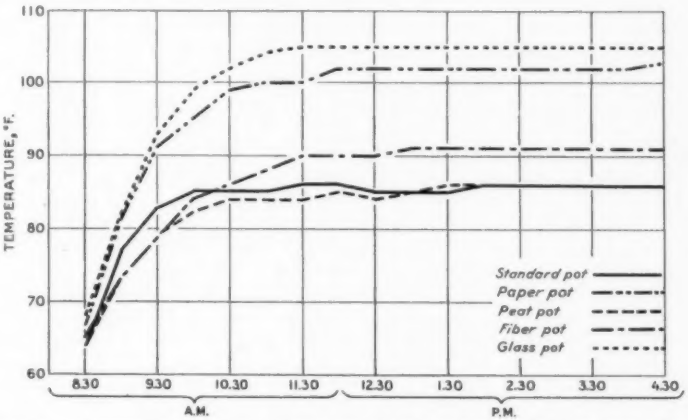

FIGURE 1.—Temperatures of soil in different types of plant containers at half-hour intervals for eight hours

TABLE 2.—*Soil temperature readings at half-hour intervals in standard pots uniformly moist and in peat pots not uniformly moist*

Time	Temperature in—							
	Standard pots				Peat pots			
	No. 1, 100 per cent moist	No. 2, 100 per cent moist	No. 3, 100 per cent moist	No. 4, 100 per cent moist	No. 1, 50 per cent moist	No. 2, 100 per cent moist	No. 3, 66 per cent moist	No. 4 100 per cent moist
	°F.	°F.	°F.	°F.	°F.	°F.	°F.	°F.
8.30 a. m.	74	75	74	74	76	75	73	72
9 a. m.	79	80	80	79	82	79	79	76
9.30 a. m.	81	81	81	81	84	81	81	78
10 a. m.	82	82	82	82	86	82	82	81
10.30 a. m.	83	84	84	83	88	83	84	82
11 a. m.	84	85	86	84	90	84	86	82
11.30 a. m.	84	86	86	86	90	86	88	84
12 m.	84	86	86	86	91	86	88	84
12.30 p. m.	84	86	86	86	91	88	88	86
1 p. m.	84	86	86	85	91	87	89	86
1.30 p. m.	84	86	86	85	91	87	90	86
2 p. m.	86	86	86	85	91	88	90	87
2.30 p. m.	86	86	86	86	93	88	91	88
3 p. m.	86	86	86	86	92	88	91	88
3.30 p. m.	86	86	85	86	91	88	91	88
4 p. m.	84	85	84	85	91	88	91	88
4.30 p. m.	82	82	82	84	90	86	88	86

Tests were made with clay pots classified according to the degree of firing in their manufacture. These are known as the soft, medium,

hard, and very hard burn. The very hard burned pot has been fired to the point of becoming vitrified and as such had soil temperatures equivalent to those found in the glass tumbler. But there was no variation in the temperatures of the soil in the soft, medium, and hard burned pots. Hence, the assumption seems justified that the cooling effect is more closely related to the area that is moist rather than to any degree of porosity. On the other hand, it is quite reasonable to state that if the element of porosity is lacking the range of temperature is related to the insulating value of the pot structure.

DISCUSSION

The data here presented show that the soil in a porous flowerpot may have a temperature as much as 20° F. below that found in soil contained in a pot of vitreous material such as glass. The vitreous pots follow, fairly closely, the air temperature of the greenhouse. The principle causing these differences of soil temperature is the latent heat of vaporization. For every gram of water that is changed to vapor about 560 gram-calories of heat are used at the air temperature that surrounded the pots during this study. A considerable proportion of the heat that reaches an evaporating surface is employed in transforming the moisture to vapor and, therefore, the mass has a slower rise in temperature than a similar mass minus an exposed moistened surface. The rise of temperature in containers that are not porous is dependent upon the insulating value of the container.

The cooling effect by evaporation is at a maximum in the porous clay pot. However, when the water of the soil in a clay pot has been reduced to the point where it can not keep the clay pot moist, the temperature of the soil will quickly rise to approximate air temperature.

Through the data presented the author introduces a physical agent altering soil temperatures which may have many applications to research work with soils in small volumes.

SUMMARY

A method was developed whereby 3-inch plant containers of different materials could be compared with each other under uniform conditions in such a manner that the effect of air temperature on soil temperature was altered by the type of construction of the container.

Pots that were sufficiently porous to produce a moist outside surface maintained a soil temperature lower than the air temperature because of the cooling effect of evaporating water.

Depending on the insulating value of their structure, nonporous containers maintained much higher temperatures than porous containers.

Containers with a part of their surface moist maintained temperatures slightly higher than those with their surfaces completely moistened.

With a uniform air temperature the temperature of soil in small containers depends upon the porosity or insulating value of the material used in the fabrication of the container, and the porous pots are also influenced by the evaporating power of the air.

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